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AN UNNECESSARY NAME-CHANGE.

BY

C. SKOTTSBERG.

Cuminia, a genus of the Labiatae, was discovered by Bertero on Masatierra (Juan Fernandez) and described in 1835 by Colla, who dedicated his new genus to the Italian mycologist H. Cumini (Plantae rariores in regionibus Chilensibus a cl. M. D. Bertero nuper detectae, fasc. VI, Mem. Accad. Torino 38: 139 tab. 47). Ever since, the name *Cuminia* has been used for this genus. However, in his »Synopsis of the South American Labiatae» (Fedde's Repert. Beih. 85: 1, 1935) C. Epling rejected Colla's name on account of the alleged existence of an older *Cuminia* J. F. Gmel. 1791, another name for *Cuminum* L., and replaced it by *Skottsbergiella* nov. nom. (*Cuminia* Colla non J. F. Gmel.). Epling failed to observe that there was already one *Skottsbergiella* Petrak 1927, a genus of Fungi described in The Nat. Hist. of Juan Fern. and Easter Island II: 481. Mr. G. Looser of Santiago, Chile, called Mr. Epling's attention to his mistake, and suggested *Johowia* as a suitable name for *Cuminia* Colla. Subsequently, *Johowia* Epling et Looser nov. nom. was published in Epling, The Labiatae of Chile, Revista Universitaria (Universidad Católica) XXII (1937) 168, with *J. fernandezia* (Colla) as typical species.

The original edition of Index Kewensis (1893), compiled under the supervision of Dr. B. Daydon Jackson, recognizes *Cuminia* Colla as valid (p. 666); it is followed by

»CUMINIA, J. F. Gmel. Syst. 309 (1791) - **Cuminum**, Tourn. (Umbell.)

Cyminum, J. F. Gmel. l. c. 484 = Cuminum Cyminum.»

There was, at that time, no international rule forcing us to drop a well-established name in favour of an older homonym even if this hadn't been taken up by anybody or had been reduced to synonymy.

The Index apparently regarded *Cuminia* J. F. Gmel. as a superfluous name-form for *Cuminum,* and allowed *Cuminia* Colla to stand, and all later authors have followed the same course until Epling discovered that there was an opportunity to make a new name. He preferred not to propose *Cuminia* Colla for conservation. The fact that Otto Kuntze, who never lost a chance to change the names of genera, did not even mention *Cuminia* in his Revisio (1891—93), passed unnoticed. In von Post and Kuntze's Lexicon, »Cuminia Gm. 1791» is treated as a synonym of »Cyminum», and *Cuminia* Colla regarded as valid. As a synonym of this, »Cuminiana OK.» is listed. I do not know where this name was first published, but this does not matter here.

For a long time I had been collecting material for a supplement to my papers on the flora of the Juan Fernandez Islands. I was puzzled by this »Cuminia» of Gmelin; why had he changed a Linnean name used in all the earlier editions of Systema Naturae? Naturally, I looked up the quotation in Caroli a Linné Systema Naturae Ed. XIII, curavit J. F. Gmelin, vol. II, Leipzig 1791. To my surprise there was no Cuminia at all: on p. 309 *Cuminum,* on p. 484 *Cuminum Cyminum!* The quotation in the Index was wrong in some way or other, either with regard to the publication or the author of the name, but I could find no *Cuminia* in the Systema Vegetabilium edited by Gmelin in 1796; this is identical with Syst. Nat. ed. XIII, and on p. 309 and 484 *Cuminum* is found, but certainly no *Cuminia.* I searched the other editions, older and later (Murray, Reichard, Roemer & Schultes, Sprengel, and so forth): the result was the same. There was the possibility that part of ed. XIII had *Cuminia* instead of *Cuminum;* this was indeed very unlikely, but I thought it better to make inquiries. I had used the copy in the library of the R. Academy of Sciences, Stockholm. I found the copy in the City Library of Göteborg identical, and answers from Kew, Lund and Uppsala gave the same result. I thought that, if ever a genus *Cuminia* had been described, either before or after Colla, it ought to be found in such general taxonomic works as De Candolle's Prodromus, Steudel's Nomenclator, Pfeiffer's Nomenclator, or Bentham and Hooker, Genera Plantarum, but it is found nowhere before the appearance of Index Kewensis in 1893. After this date *Cuminia* J. F. Gmel. turns up in works where an ample list of synonyms is supplied, as in Dalla Torre & Harms, Genera Siphonogamarum

(1900—07) 370, Das Pflanzenreich (IV: 228, 1910, WOLFF, Umbelliferae 358: »ex. Ind Kew.»), and HEGI's Flora V: 2 (1926) 1138; finally, in EPLING's papers. In every case, Index Kewensis is the original source. But the statement is false, J. F. GMELIN never used the name *Cuminia*, either for *Cuminum*, or for any other plant; all that is left is Cuminia Ind. Kew. nomen nudum.

How did such an entry ever get into the Index? I asked Dr. W. B. TURRILL, Keeper of the Kew Herbarium, who kindly answered: »The reference in the original Index Kewensis is wrong, and I suspect happened as a result of bad handwriting on the original slips.» It didn't seem clear to me why Dr. JACKSON ever wrote a slip for *Cuminum* with GMELIN's name on, but if he did, he must have had a slip for every reference, and then have picked out what was needed for the manuscript. In doing so, he, or rather the person who assisted him, happened to read »Cuminia» — but who added »= Cuminum Tourn. (Umbell.)», and the rest of the entry? I can offer no explanation of how this happened, nor does Dr. JACKSON's account of how the Index was prepared (Journ. Bot. 25 (1887)60) give any information. I have discussed the matter with Mrs. T. A. SPRAGUE, for many years on the staff at Kew and a specialist on the Index work. Mrs. SPRAGUE kindly advised that Dr. JACKSON's original manuscript should be consulted. Unfortunately, this could not be done; Dr. TURRILL informed me that, as far as he was able to ascertain, the manuscript had been destroyed during the war; not, however, by enemy action.

This somewhat lengthy discussion shows that, in cases, it is better to control a statement even in a codex like Index Kewensis. The result of my little investigation can be expressed thus: **Cuminia** Colla 1835. Syn.: *Skottsbergiella* Epling 1935 non Petrak 1927; *Johowia* Epling & Looser 1937.

An unhappy consequence of Dr. EPLING's action is that the name *Johowia* cannot be taken up again. It is easy to understand that Mr. LOOSER, to whom I am obliged for kind assistance, wanted to commemorate the botanical work of Dr. F. JOHOW by dedicating a plant genus to him. To JOHOW we owe the important monograph »Estudios sobre la flora de la Islas de Juan Fernandez», a posthumous »Flora de Zapallar», and other papers. Mr. LOOSER cannot be blamed for the unhappy result of his praiseworthy intention to honour a prominent botanist and compatriot.

Svensk Botanisk Tidskrift. Bd 45, H. 1. 1951.

PROBLEMS IN THE CLASSIFICATION OF THE MARINE ALGAE.

BY

GEORGE F. PAPENFUSS.

In a paper given in 1926 at the Fourth International Botanical Congress, assembled in Ithaca, Professor Svedelius remarked: »... one of the most important of the newer points of view as I take it, is the place in the life-cycle where the reduction division occurs, this again being also connected with the alternation of generations which, I hold, must be regarded as a very important element in determining the relationships of plants.»

Although, as would be expected, knowledge of the life histories has not in all instances furnished the answer to problems of relationship, the vast amount of new information concerning the methods of reproduction and the cytology of algae that has been acquired during the past twenty-five years has been of immeasurable assistance in the interpretation of phylogenetic affinities, and it hence has been necessary to revise the systems of classification of various groups of algae.

The objectives of the present paper are twofold: to review briefly the present systems of classification of the higher categories in the green, brown and red algae and to suggest certain modifications in these systems.

Chlorophycophyta.

Large gaps still remain in our knowledge of the life histories and cytology of the green algae. Although method of reproduction and life history are of importance in the delimitation of certain orders, somatic organization plays a much more important rôle in the division of this phylum into orders. It is now well established that the same type of life history has arisen independently in different lines

of development (e.g., an alternation of isomorphic generations as in the *Ulvales* and *Cladophorales;* the diploid phase functioning as the gamete-producing generation as in the *Siphonales* and *Dasycladales*).

Much disagreement still exists as to the number of orders which constitute the *Chlorophycophyta* and the position of some of the families and genera. As a basis for discussion I present a system of classification of the orders of the green algae (fig. 1) which departs in certain major respects from those currently in use. This system combines certain features of the systems of FRITSCH and SMITH, and incorporates the conclusions of Miss EUBANK, presented in a thesis (as yet unpublished) at the University of California in 1949, with respect to the so-called siphonous green algae. Eleven orders are recognized: *Volvocales* (including *Tetrasporales* of some authors), *Zygnematales, Ulotrichales* (including *Chaetophorales* of some authors), *Oedogoniales, Schizogoniales, Ulvales, Chlorococcales, Cladophorales, Siphonocladales, Siphonales, Dasycladales.*

The *Volvocales* are regarded, in agreement with the consensus of opinion, as the ancestral group from which have evolved the *Ulotrichales, Chlorococcales* and possibly the *Zygnematales.* The *Ulvales* and possibly also the *Oedogoniales* and *Schizogoniales* are conceived as having evolved from the *Ulotrichales.* The *Cladophorales, Siphonocladales, Siphonales* and *Dasycladales* are believed to have evolved as independent lines from the *Chlorococcales.*

The general structure of the cell of members of the *Tetrasporales* is in close agreement with that of members of the *Volvocales* and it seems best to unite these two orders. Although the *Volvocales* are characterized by the possession of flagella in the vegetative condition as contrasted with the non-motile nature of vegetative individuals of the *Tetrasporales,* certain species of *Chlamydomonas* possess non-motile, palmelloid stages. The *Zygnematales* and *Oedogoniales* stand well apart from the other orders of green algae. The *Schizogoniales* possess stellate chloroplasts and, what is especially important, parenchymatous thalli. The order is accepted by KNEBEL (Hedwigia 75: 1—120, 1935) in his monograph of the group. The *Ulvales,* like the *Schizogoniales,* are characterized by the possession of parenchymatous thalli, a feature exhibited even by so simple a member as *Percursaria.* Certain species of *Ulva* and *Enteromorpha* show an alternation of isomorphic generations.

The order *Chaetophorales,* which is merged in the *Ulotrichales,* is based essentially on the heterotrichous habit of the thalli. How-

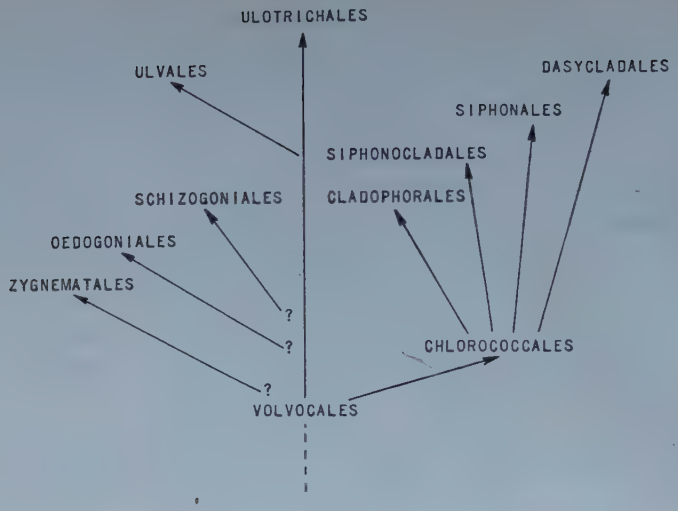

Fig. 1. Diagrammatic representation of the probable interrelationships of the orders of the green algae.

ever, in *Draparnaldia* and *Draparnaldiopsis,* two of the most highly evolved genera in the *Chaetophoraceae,* a prostrate system is practically lacking. Moreover, in *Sporocladus* and certain other genera ordinarily placed in the *Chaetophorales* a prostrate system is completely lacking. Members of the *Chaetophorales* usually possess a branched thallus, as contrasted with the unbranched thalli of members of the *Ulotrichales,* but even in *Ulothrix* the thallus at times is branched.

In the *Chlorococcales* the cells are multinucleate and the chloroplasts are frequently poorly organized with the photosynthetic pigments diffuse in the peripheral cytoplasm. No vegetative cell divisions occur in this order. The majority of forms appear to be haploid, but there is some suggestion that *Chlorochytrium Lemnae* shows an alteration of generations (Kurssanov & Schemakhanova, Arch. Russ. Protistol. 6: 144 –146, 1927) and that *Apiococcus consociatus* is diploid (Korshikov, Arch. Protistenk. 55: 439—503, 1926).

Members of the *Cladophorales* have multinucleate cells with ill-defined reticulate chloroplasts. Growth is frequently apical. Some genera show an alternation of isomorphic generations, whereas certain species of *Cladophora* apparently are haplobiontic diplonts. Miss Eubank would derive this order from the *Chlorococcales.*

In the *Siphonocladales* the thallus is septate as the result of segregative division of the protoplasts. The segments are multinucleate and the chloroplasts are in the form of a reticulum composed of a series of polygonal plates. The plants are diploid or the life history includes an alternation of isomorphic generations.

The *Siphonales* have a non-septate and, as far as known, diploid thallus. They contain the xanthophylls siphonein and siphonaxanthin in addition to those present in other green plants (STRAIN in FRANCK & LOOMIS, Photosynthesis in Plants, 1949). This order may have evolved from diploid *Chlorococcales* and may thus have been composed of haplobiontic diplonts from the time of its inception.

The *Dasycladales* comprise one of the most clear-cut of all orders of green algae. The thallus is uninucleate, except possibly in *Cymopolia* (HÄMMERLING, Arch. Protistenk. 97: 7—56, 1944), and diploid. It consists of a central siphon from which issue verticillately arranged laterals which produce, in many forms, a sort of cortex about the axis. Within the gametangia are formed, in the majority of forms, a number of operculate cysts inside of which the gametes are produced.

Phaeophycophyta.

KYLIN'S (Lunds Univ. Årsskr., N. F., Avd. 2, 29, No. 7, 1933) system of classification of this phylum, as slightly modified by PAPENFUSS (Bull. Torrey Bot. Club 74: 398—402, 1947), is founded to a large extent upon life histories. Three classes, *Isogeneratae, Heterogeneratae* and *Cyclosporeae,* are recognized. The *Isogeneratae* include algae which show an alternation of isomorphic generations and they are arranged in the five orders *Ectocarpales, Sphacelariales, Cutleriales, Tilopteridales* and *Dictyotales.* The *Heterogeneratae* contain the two subclasses *Haplostichineae* and *Polystichineae.* In the *Haplostichineae* the thallus is pseudoparenchymatous, consisting of coherent filaments. This subclass includes the orders *Chordariales* and *Sporochnales.* In the Polystichineae the cells of the thallus divide by intercalary longitudinal walls, hence true parenchymatous tissues are produced. This subclass is composed of the orders *Dictyosiphonales, Desmarestiales* and *Laminariales.* The class *Cyclosporeae* contains but one order, the *Fucales,* whose members are all haplobiontic diplonts.

The chief objections to the system of KYLIN are that: (1) It

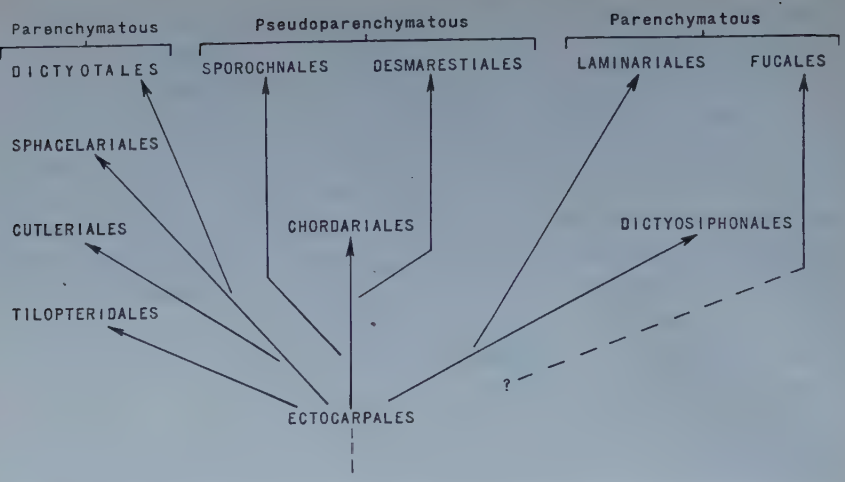

Fig. 2. Diagrammatic representation of the probable interrelationships of the orders of the brown algae.

precludes the possibility of parallel and independent evolution of groups with an alternation of isomorphic or heteromorphic generations. (2) It does not allow recognition of the *Ectocarpales* as the possible ancestral stock from which have evolved various other groups of brown algae. In view of the close agreement between members of the *Ectocarpales* and representatives of certain other orders (e.g., *Myrionemataceae* in the *Chordariales*) such a relationship appears highly probable. (3) It obscures the fact that the *Fucales* as well as certain groups in the *Isogeneratae* (e.g., *Sphacelariales, Dictyotales*) are polystichous.

The system portrayed in figure 2 is presented as a basis for discussion.

Rhodophycophyta.

This phylum is composed of two groups, the classes *Bangioideae* and *Florideae*. The *Bangioideae* have been separated by Kylin into the two orders *Porphyridiales* and *Bangiales* on the basis of the absence or presence of sexual reproduction, but this division may not be a natural one.

A new era in the classification of the *Florideae* started in 1923 when Kylin refined the ideas of Schmitz and produced a system based on the auxiliary cell. This system reached its culmination in 1932 in his paper on the order *Gigartinales* and has been in general

use since that time. According to KYLIN the *Florideae* may be divided into six orders as follows:

I. Typical auxiliary cells not produced.
  A. Haplobiontic ..... *Nemalionales*
  B. Diplobiontic ..... *Gelidiales*
II. Typical auxiliary cells produced.
  A. Auxiliary cells formed before fertilization.
    1. Auxiliary cells in special accessory branches or clusters of branches ..... *Cryptonemiales*
    2. Auxiliary cell an ordinary intercalary cell of the thallus ..... *Gigartinales*
    3. Auxiliary cell formed by a daughter cell of the supporting cell toward the surface of the thallus ..... *Rhodymeniales*
  B. Auxiliary cell cut off from the supporting cell after fertilization ..... *Ceramiales*

Inasmuch as the typical auxiliary cell of KYLIN, or the generative auxiliary cell as it should perhaps be called, is the starting point of a generation, the carposporophyte, there can be little question that the presence or absence of this cell, its time and manner of formation, and its position with reference to the carpogonium are matters of the utmost importance in the classification of *Florideae;* and few if any will dispute the fact that the system of KYLIN allows of a much more natural grouping of the *Florideae* than had previously been possible. However, any system of classification is to a certain extent based upon the interpretations of its author and upon the knowledge available at the time of its publication, and is hence subject to modification.

Although the *Nemalionales* as delimited by KYLIN appears to be a perfectly natural group, the separation of this order from the majority of other orders on the basis of a haplobiontic life cycle and the absence of an auxiliary cell is not entirely correct. In *Scinaia, Asparagopsis, Chaetangium* and *Galaxaura,* one or more cells in the carpogonial branch function as the generative auxiliary cell, as has been pointed out by SVEDELIUS (Nova Acta Reg. Soc. Sci. Upsaliensis, Ser. 4, 13, No. 4, 1942) and MARTIN (Jour. Linn. Soc. London, Bot. 52: 115–144, 1939). Furthermore, at least three genera of this order *(Audouinella, Galaxaura* and *Actinotrichia)* are diplobiontic or include diplobiontic species, and the fact that *Audouinella* is

representative of the least advanced family, the *Acrochaetiaceae,* is significant. However, as all students of the *Nemalionales* will agree, even these diplobiontic forms in both vegetative structure and the morphology of the reproductive organs agree very well with their haplobiontic relatives.

Generative auxiliary cells have a dual function—they furnish nutritive materials and generate the gonimoblast. In certain *Florideae,* notably in the *Gelidiales,* but also in some *Cryptonemiales (Polyides)* and *Gigartinales (Cruoria),* the rôle of the auxiliary cell is that of nutrition only, the gonimoblast developing from the ooblast filament following the establishment of a connection with an auxiliary cell. Although these auxiliary cells (nutritive auxiliary cells) do not serve as the starting point of the gonimoblast, they are nevertheless essential to its development, and frequently, as in the *Gelidiales,* they are morphologically well differentiated. Generative auxiliary cells may conceivably have evolved from nutritive auxiliary cells such as found in the *Gelidiales.*

In this connection it is of interest to note that members of the family *Dumontiaceae* of the order *Cryptonemiales* possess both nutritive and generative auxiliary cells, the former being located in the carpogonial branch or its derivatives, and the latter some distance away from the carpogonial branch. In the *Weeksiaceae,* a family recently established by Mrs. Abbott in a thesis (as yet unpublished) presented at the University of California, the nutritive auxiliary cell which is located in the carpogonial branch has become the generative auxiliary cell. In *Sphaerococcus,* which Kylin placed in the *Gigartinales,* the auxiliary cell is an accessory supporting cell, a feature characteristic of the family *Kallymeniaceae* in the order *Cryptonemiales.*

From the preceding remarks it will be clear that the orders *Nemalionales, Gelidiales, Cryptonemiales* and *Gigartinales,* are not as sharply definable as would appear from the system of Kylin. However, it is equally clear that little can be done toward an improvement of the system of Kylin until we know a great deal more about the comparative development of the red algae. The *Cryptonemiales* and *Gigartinales* are especially marked by seemingly overlapping types, but whether these types represent a true relationship or merely instances of parallel evolution cannot at present be determined.

Pending further knowledge concerning the developmental morphol-

ogy of the red algae, the key of KYLIN to the orders of the Florideae may be modified as follows:

I. Genera with few exceptions haplobiontic.
Gonimoblast developing directly from the fertilized carpogonium or from one (or more) of the other cells of the carpogonial branch which functions as a generative auxiliary cell ..... *Nemalionales*

II. Genera with few exceptions diplobiontic.

A. Gonimoblast developing from ooblast filaments following their fusion (?) with nutritive auxiliary cells ..... *Gelidiales*

B. Gonimoblast usually developing from a generative auxiliary cell which with few exceptions is not a cell in the carpogonial branch, or rarely gonimoblast developing from an ooblast filament following a fusion with a nutritive auxiliary cell.

1. Generative auxiliary cell usually produced and always initiated before fertilization.

a. Generative auxiliary cell in a special accessory filament or cluster of filaments, or rarely in the carpogonial branch; or in the Kallymeniaceae the accessory supporting cell functioning as an auxiliary cell; or gonimoblast rarely developing from an ooblast filament ..... *Cryptonemiales*

b. Generative auxiliary cell an intercalary cell of a vegetative filament (except in *Sphaerococcus*); or gonimoblast rarely developing from an ooblast filament .... *Gigartinales*

c. Generative auxiliary cell always produced and always initiated by a daughter cell of the supporting cell toward the outside of the thallus ..... *Rhodymeniales*

2. Generative auxiliary cell always produced and always initiated by the supporting cell after fertilization ..... *Ceramiales*

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A CONTRIBUTION TO THE HISTORY OF THE HAWAIIAN VEGETATION.

BY

OLOF H. SELLING.

In a preliminary communication (Selling 1949) I promised a reply to Fagerlind's contribution (1949) to the interpretation of my Hawaiian pollen diagrams, a contribution which at the time I could only briefly characterize. I was engaged in field work at the farthest point of my travels in the South, and for long unable to comment properly.

Fries' review (1949) — though not dealing with much of the evidence provided by local phytogeography — altered the situation; here spoke an author with personal experience of pollen statistics. A detailed reply to Fagerlind after that did not seem as urgent, more especially as soon afterwards other authors published additional confirmations of one or more of my theses (Firbas 1949, Chiarugi 1950, Schwarzbach 1950). One of my cardinal points was also tested on purely meteorological grounds, and confirmed (Leopold 1949).

Now the time has come for a proper reply, however.

I. General Remarks on Fagerlind's Criticism.

In my preliminary communication I remarked that Fagerlind's criticism does not give a correct picture of what I have clearly stated in my 1948 paper. It need not be stressed that it is hardly compatible with scientific custom in a criticism to devote, without any acknowledgment whatever, long paragraphs to ideas which are already brought out in the criticized work. I am not thinking so much of Fagerlind's remarkable introduction, but, *i.a.*, of his

discussion of conditions in West Maui (Fd[1], middle of p. 80). One gets the impression that Fagerlind has introduced something new in the discussion when speaking of »the varying distance» which »explains straight away the differences». This is not the case. On the contrary, I have clearly appreciated this alternative (Sg, p. 108, line 10 ff. from the bottom) but by weighing it against the other I have — as will be shown below — come to a more differentiated opinion. The same applies to what Fagerlind says of my having »elected to ignore» the sources of error I have pointed out. These examples might be multiplied; I will revert to them below.

II. The planning of my Hawaiian investigations.

I pass to Fagerlind's directions in the paragraph on p. 74 commencing »As the Hawaiian peat was not previously known . . .»[2]. Fagerlind says that it would have been »most profitable» for me to have taken a series of »parallel bore samples» in »one and the same limited mire area» and compared the results. He speaks of the »absence of comparison material so collected». This is incorrect (comp. Sg, p. 73, lines 3 and 4 from the bottom). The four groups of stations which he mentions as if he had discovered them, were actually selected for that very purpose, and the amplitude of the variation in these series (which Fagerlind is not the first to point out; see Sg, p. 90) was what made me limit my discussion to the main features of the vegetation history. Fries has observed this (1949, p. 348), but Fagerlind has not. Fagerlind's point of view has been taken over from Swedish workers for whom it may sometimes be justified. The very obvious reasons for which in this particular case it loses its value may be summarized thus:

1) In an environment as mountainous (see Fig. 1), and meteorologically and phytogeographically varying as that of the Hawaiian Islands, the results of detailed comparisons obtained in one restricted mire area can not be applied to another. To be of any value — in dealing with general features — such a comparison requires closely corresponding environment over large areas.

[1] In the following Fagerlind 1949 is abbreviated »Fd»; Selling 1948: »Sg».

[2] Hawaiian peat has been known for more than a century, not its pollen-statistical possibilities, however.

Fig. 1. Valley topography of the windward side of West Maui, Hawaiian Islands. Upper parts of ridges hidden in clouds. Several mires of West Maui are situated at the heads of valleys like this, which is one of the tributaries of the Iao Valley. — Photograph by the author, 6.VIII.1938.

2) I was investigating the main features of the vegetation. For this purpose the material collected was sufficient. A more local analysis of the sort referred to by FAGERLIND would have meant abandoning the most important part of my investigation — regional research — in favour of purely local problems. Under the circumstances governing my work, this would have been a mistake indicating lack of appreciation of essentials.

III. Sources of error.

a. Production and dispersal of pollen.

FAGERLIND — and incidentally also FRIES — calls for a more detailed discussion of the significance of pollen dispersal to the appearance of the pollen diagrams than I have given in Parts II and III. What FAGERLIND is saying, however, confirms the futility of any such discussion at the present time, and it is just because I knew this that I planned my text as I did. FAGERLIND is »quite sure» that *Acacia*, which has clumsy pollinia, would produce »pollen clouds with extensive dispersal», and refers the genus to the same category as *Metrosideros*, which has small, light pollens. I

myself have stressed, and FAGERLIND has repeated, the truth that the *Metrosideros* curve has undoubtedly been influenced by the local *Metrosideros* thickets on the mire. But – and this is the important point — one cannot reasonably assume that the pollen rain from these local thickets has been able to hide the main features of the enormous masses of pollen from the forests – *Metrosideros* is the dominant tree in the rain forests of the Hawaiian Islands. And my paper deals with nothing but the main features.

FAGERLIND (p. 74) asserts that *Myrsine* and *Pelea* in the rain forest, in contradistinction to for example *Myrsine* in drier places and in the mires, cannot very well be supposed to be particularly well represented in the pollen rain, »on the one hand, owing to their floral structure and the placing of their flowers and, on the other, owing to the construction of the rain forest communities». But the *Myrsine* species on dry ground have after all the same floral structure as those in the rain forest, and the placing of the flowers of the latter species certainly does not prevent wind dispersal — to say that it does shows inadequate observation of nature. This the more as the broken topography of the Hawaiian rain forest areas often makes the flowering branches of the trees very well exposed to the wind. On the other hand I have never considered *Pelea* one of the producers of large pollen clouds. This is apparent already from my diagrams, in which for that very reason I have not included more than *Pelea* of Type II — the other is of too local a nature — and have not ascribed to this irregular appearance of *Pelea* in the diagrams any particular phytogeographical significance. The irregularities stressed by FAGERLIND (p. 74) in the above-mentioned discussion of local investigations are accordingly of very slight importance indeed. His conclusion that more or less all the *Pelea* pollen in the diagrams has come from the mire vegetation is unfounded. He draws the same conclusion in respect of *Myrsine*: it is, according to him, »extremely probable» (!) that the pollen found in the mire »originates *entirely or almost entirely from plants of the mire* and not from the components of the forest» (italics by O.S.). What has been said above of the chances of its pollen being dispersed applies to this. Moreover, FAGERLIND should after all have observed that the *Myrsine* pollens make up 28 % of the entire pollen flora of the diagrams (SELLING 1947, p. 252) having reached this value in competition with the production of the forest. *Myrsine* is also one of the most important forest trees in these

levels (Sg, p. 41, 84, and 95), next in importance to *Metrosideros*, and would still be »entirely or almost entirely» represented by the few shrubs in the mire»! The same can be said of *Metrosideros* —: is it even possible that the pollens from the limited mire vegetation can — generally speaking — compete successfully with the enormous masses produced in the vast areas of forest trees?

Fagerlind's conclusion that practically all the *Coprosma* pollen has also come from the mire vegetation is likewise untenable. The reason given is that »as a rule» the rain forest representatives of this genus »hardly» belong to the higher stratum.

The *Coprosma* species are good examples of anemophilous plants (see further Selling 1947, p. 316). In the broken topography they have ample opportunities of pollen dispersal, even when they are solely rain forest species of low trees. The *Coprosma* culminations to which I have ascribed importance are, moreover, obviously not extreme rain forest species, but species growing peripherally in the forest. This is a conclusion to which I have been forced by the diagrams, as the available literature gave very little information on this point. It was therefore all the more interesting, on a visit to Hawaii in 1949, to learn from Mr. O. Degener and Professor H. St. John, the foremost experts on Hawaiian plant distribution, that they had in a number of localities, just at the periphery of the rain forest, found that more than 50 % of the tree storey were of *Coprosma*. Rock's description of the peripheral rain forest above Naalehu, Hawaii, as consisting mainly of *Coprosma* and a few other genera (see Sg, top of p. 97) should here be kept in mind. These observations confirm my interpretation of the diagrams, and the rather irregular occurrence of these peripheral stands of *Coprosma* also explains why considerable frequency variations may be expected in the diagrams, even if these are derived from adjacent localities. I may here quote Selling 1947, p. 316:

»In certain periods characterized by transitions between ± dry forests and extreme rain forest there are regular peaks of *Coprosma*, indicating beyond doubt that one or more species of this genus did play a decided part in the vegetational succession.»

And above all this:

»It is essential to bear in mind that local scrub vegetation, though playing a certain part in the curves, evidently does not suppress their major characteristics.»

These statements have now gained strength.

b. Differential pollen destruction.

So much for FAGERLIND's discussion of the influence of pollen dispersal on the diagrams. He goes on (p. 75) to another of the sources of error I have mentioned — differential pollen destruction —, and tries to obtain a concrete idea of its importance, but only succeeds by disregarding other possibilities. The fact that the analyses from Sta. 33 contain about 60 % more pollen than those from Sta. 34 can definitely not be regarded as proof of differential destruction as long as we do not know anything about the variations in pollen supplies. The only thing we do know for certain is that these are considerable in this particular spot, where the swampy depression emerges in the valley below, the topography of which is also very broken (comp. Fig. 1). FAGERLIND's gradation of the effect of destruction on the pollen of the several genera is pure guesswork. FAGERLIND's ideas can only be deemed of value to the interpretation of Diagram 34 if we disregard the fact that they completely fail to explain corresponding cases elsewhere. One need not examine the diagrams very closely to prove this. I will deal below (p. 24–30) with the confirmation which FAGERLIND thinks he has found in Diagram 81.

In this case, too, it is obvious that in our present state of knowledge detailed discussions of the kind introduced by FAGERLIND will end where they begin. The statements »Pollen destruction is presumably not a phenomenon peculiar to the Hawaiian world. Aspen pollen is not found in our peat and ooze formations» (FD, p. 75) reveal his lack of familiarity with the subject. It is common knowledge that pollen destruction occurs outside Hawaii. His assertion that aspen pollen is not found in »our peat and ooze formations» is incorrect: IVERSEN (1946) has made it likely that aspen pollen has so far been confused with cyperaceous pollen.

My conclusion regarding the relative ages of the lower portions of Sta. 34 is thus not affected by FAGERLIND's arguments on p. 75.

The proofs of the efficacy of destruction deduced from the actual diagrams having thus been confuted, there remains an examination of the environmental evidence. Turning to a source of error that I have already pointed out, viz. »destruction of pollens by trickling water rich in oxygen» (SG, p. 90), FAGERLIND says that »it is evident that a soligeneous mire surface with a supply of water comparatively rich in oxygen must be characterized by greater pol-

len destruction than an ombrogeneous one». I do not find it »evident». Rain water impinging on a mire surface is certainly rich in oxygen, and it will thus be a question of comparing the duration of its effects in the two cases. This is a matter which cannot be settled at the writing desk — Hawaiian rains in these altitudes are not comparable to rains in Sweden, and there is also the question of how much Hawaiian peats have become aerated. I therefore — contrary to FAGERLIND — prefer to leave the question open, as I did in my paper of 1948, more particularly as the other equations affecting these facts (not least the expositional) contain many unknowns.

c. General summary regarding the order of magnitude of the several sources of error.

In concluding this part of the discussion, FAGERLIND himself seems to have realized that he has ended up in a blind alley. He writes (p. 76) that it is naturally impossible to come to any definite decision regarding the interrelations of the sources of error to which he has devoted 2 1/2 pages. This conclusion is the same as mine (SG, p. 90). FAGERLIND continues:

»Nor is a decision on this matter really of primary importance. What is of importance, on the other hand, is the following affirmation: *The diagrams published by* SELLING *illustrate in a high degree local conditions. They hardly give a correct picture of the history of the forest-tree vegetation.*»

This reasoning is illogical, and the conclusion clearly false.
I repeat my own words (SG, p. 90):

»Important is, however, that, despite these [= the above] and other conceivable limitations, the diagrams show the same general development. The good agreement justifies the conclusion that changes common to all the islands are without serious local disturbances registered in this combination of pollen curves. These pollen diagrams can be used with good success in establishing the main phases of the vegetational development.»

This is as applicable as ever, and I will give further proofs below.

IV. The relation rain forest — dry forest.

FAGERLIND's next objection refers to the relation rain forest — dry forest. He designates as »unsound» (p. 76) my conclusion that the border separating districts of these two types of forests has

moved. He thinks that the border may just as well have been stationary, but that the composition of the dry forest alone has been subjected to changes. This is an intrinsically improbable — and if we go further into the subject absolutely impossible — postulate. FAGERLIND writes (l.c.): »The course of the curves in diagram 34 b *can thus signify* [italics mine] that the xerophyte vegetation during one period (Period III[1]) contained more *Dodonaea* and *Acacia*, and during another period (Period I[2]) more *Chenopodium*». The expression »can thus signify» is meaningless, seeing that there can be no hesitation about qualitative local differences in the periods I and III, whether these are due to differences in altitudinal belts, conditions of colonization, or other factors. I noted this myself, and — what is more — published the same diagram excluding *Chenopodium* (SG, Fig. 26, p. 102; here reproduced in Fig. 2) to show that the major tendencies nevertheless persist.

With this FAGERLIND arrives at the idea that the rain forest period (Per. II) might possibly be apparent only: »It is by no means out of the question that plant types without great pollen dispersal capacity were the dominants in the xerophytic forests during the intermediate period (Period II), or that *Sophora-Myoporum* forests were then more sparsely populated by *Dodonaea* and *Chenopodium*.» In that case, how about *Acacia*? This would have spoken for itself about other changes having taken place, and other species would have contributed to the same interpretation. FAGERLIND's objection is purely philosophical, and valueless as an alternative to my interpretation. One might furthermore ask: If it is only a question of changes in the dry forest without any changes in humidity (which automatically affect the area of the rain forest), *why should peat formation then be concentrated to Period II?* Should not equally ample peat formation rather be expected all along the line in Period I? How is one — with real knowledge of local conditions — to conceive the revertent succession of the leading rain forest elements (see Figs. 3, 9, 12 of the present paper, and other diagrams in SG, Pls. 24–27) without any changes in humidity? FAGERLIND's reasoning leads to absurdities, and absurd is also his italicized assertion that I would have come to »an entirely different conclusion . . . if *Chenopodium* (or some other element among these that dominate in his [O. S.] investigation) had possessed the same floral organiza-

[1] Should be I.
[2] Should be III.

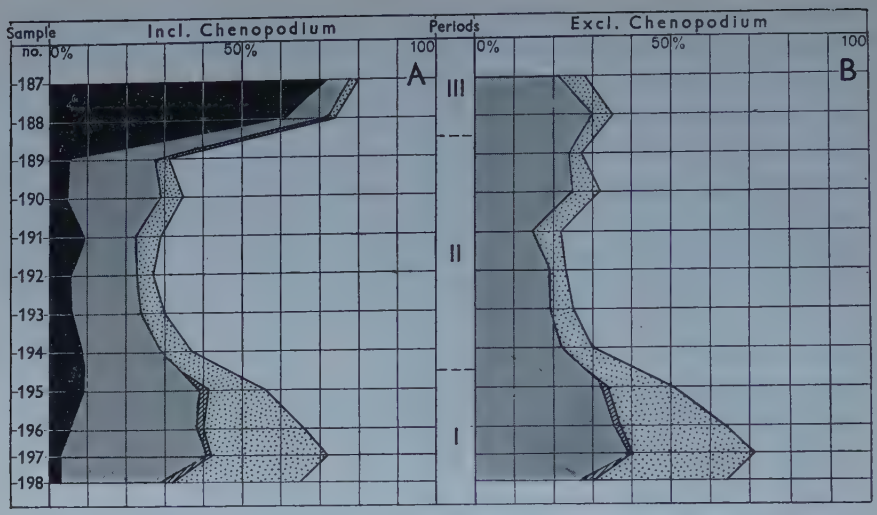

Fig. 2. Detail of Diagram 34 from West Maui, near summit (= SELLING 1948, p. 102, Fig. 26). Values with *Chenopodium* included in (A) and excluded from the 100 % sum (B) for comparison between Periods I and III (see middle column). Black: *Chenopodium*. Cross-hatched: *Dodonaea*. Ruled: *Sophora*. Dotted: *Acacia*. — In spite of the exclusion of *Chenopodium* the main tendencies of the three periods persist. HANSEN's diagrams from the Pacific Northwest (1947) and many others offer beautiful comparisons with Diagram B. See further Figs. 9–11.

tion as *Sophora*». »Some other element» is an addition which does not make this reasoning better. For even if *Chenopodium* and some other element (or elements) had had »the same floral organization as *Sophora*», that is, if they had belonged to Papilionaceae (!), *my conclusion would not have been different*. Large changes in nature do not take place without leaving traces of some kind. Since every Hawaiian vegetation belt contains a set of ± anemophilous plants, the main *tendencies* of the vegetational development can always be detected. FAGERLIND seems again to have overlooked that pollen statistics is a science dealing with relative values, and that I have not aimed at anything else. *Sophora* and *Myoporum* could have been left out of the diagrams without altering the result under discussion; it would only have meant cutting off the possibilities of gaining an idea about the frequency changes of the two genera as compared with other xerophytic (and ± mesophytic) representatives. [I included them in the diagrams in spite of their very sparse representation and slight dispersive ability, and it is significant that *Sophora* reaches values above 1 % only in Period I, when all »dry forest» elements except *Chenopodium* reached their maximum values

(see Fig, 2, samples 195—198) and the nowadays dominant rain forest was farthest displaced from the locality concerned. Just because of its slight pollen dispersal, *Sophora* contributes to confirm my conclusion that the drier types of vegetation were not far away, a conclusion which will be further dealt with on p. 31—35.] It should be pointed out that vegetation types outside the typical rain forest areas have been traced not only with tree pollen, but also with the pollens of other species. In Period I on Puu Kukui (Diagram 34) there is thus grass pollen with amounts corresponding to 47 % of the total tree-pollen flora of the diagrams. The appearance of grass pollen in such frequencies is not compatible with the assumption that the present local conditions, with rain forest and mire, were obtaining; grasses do not play such a significant part in these areas.

What FAGERLIND has to say of the relation of xerophytes and hygrophytes in for instance *Metrosideros* and *Myrsine* has already been said by me (SG, p. 76), and has nothing whatever to do with the main features of the diagrams. His italicized conclusion (FD, p. 77) that my diagrams do not give a true picture of the relations of rain forest to dry forest is correct only if one imagines that other conclusions than in regard to developmental *tendencies* can be drawn from each of them. As an objection to my text it is wide of the target.

V. The division into periods.

The most remarkable part of FAGERLIND's criticism is that dealing with the division into periods.

As to his assertion: »There is no proof whatever that the three periods really existed» (p. 77), I will make the introductory remark that few examples of a corresponding mistake can be found in the literature on Quaternary vegetation research.

The following alone will suffice to illustrate this. At for instance the summit of West Maui — in our days one of the wettest areas on earth — Period III is characterized by the mass appearance of Chenopodium oahuense, a dry-district plant. Its pollen suddenly reaches a dominance of 80 % of the aggregate pollen production of all the forest trees of the diagrams, including the mass production of Metrosideros. At the present time Chenopodium is extremely rare in West Maui, and is only known in two collections.

DEGENER, who at my request bore this species in mind when collecting inside and outside the rain forest on the leeward side of West Maui in the summer of 1949, did not even find a trace of it (letter of 28 Dec., 1949).

Facts like these cannot be overthrown.

Moreover, *it is not a matter of chance that the Hawaiian diagrams agree closely with diagrams from other areas, and that they find their natural explanation from both phytogeographical and meteorological points of view.* I will partly revert to this below (p. 34). I do not find it necessary, however, here to reiterate how *my interpretation naturally fits into the picture of the North Pacific circulation system, a question not touched by FAGERLIND.* The reader is here referred to my paper of 1948 (middle of p. 121, and p. 25–27).

It should be emphasized that the lower limit of Period III is not by any means, as asserted by FAGERLIND, defined solely by the quantitative relation of *Chenopodium* pollen to other »forest tree pollens», even if this relation is illuminating enough on for instance West Maui. My discussion of the limits of this period shows that my procedure has not been so very schematic, but that I have tried to reach an interpretation based on the general rhythm of the diagrams, independent of floristic (and possibly metachronous) features in the shape of occasional culminations; and where there are uncertainties, I have indicated their presence by queries of different sizes acc. to degree of uncertainty. My Fig. 26 (p. 102; reproduced in p. 20 of the present paper) also shows that my division into periods holds good even if *Chenopodium* is left out. Diagram 34 is not »dubious», but can be used quite well for a division into periods of this kind. It cannot be denied that this locality retained its soligeneous character as long as peat was forming there, and if percolating water has resulted in differential pollen destruction, similar conditions have at any rate obtained throughout, and the general tendency of the curve remains the same. The assertion that my dating of Period I in this diagram is »unsound» is completely unfounded. This is evident if my text is read with any kind of sound judgment and compared with the works quoted by me in 1948 on p. 117 (e.g. HANSEN 1947), and is moreover beautifully confirmed by the combined diagrams in FRIES 1949 (see below, Figs. 11 and 12). FAGERLIND's talk of »the alleged fluctuation in the relation between the distribution of the elements of the xerophytic and rain forest» (p. 77) has already been elucidated.

VI. Details of Period II.

a. General remarks on the *Metrosideros* curve and humidity conditions.

FAGERLIND's conclusions on *Metrosideros* (p. 77–78) have led him astray. He asserts that we know nothing about where to look for the culmination in Period II. This can certainly not be decided from a diagram selected at random. Such must be taken as are, by their smoothed values (e.g. 34) or perfect revertence features (e.g. 81), able to give a picture of the development which is as far as possible undisturbed by local variations. In these diagrams, the culmination - which is not necessarily at the middle of the rain-forest period (Period II) — can without any great difficulty be found at the point where the aggregate pollen curves of the rain forest trees reach their highest values, or their longest sequence of maximum values. When we then find that the shape of the *Metrosideros* curve is symmetrical on both sides of this culmination (see sample in 140 cm depth in Fig. 3, p. 25), we are in my opinion justified in saying, as I have done, that this curve is »the nucleus around which those of the other species of the main diagram are grouped». FAGERLIND's statement regarding »the fallacy of this passage» is ill-considered.

But he is not content with that. *Metrosideros*, the dominant tree of the wettest rain forest, becomes in his reasoning »not . . . an indicator of great, but of relatively low humidity». He has italicized this on p. 78. It is true that we have no »knowledge» — if by that we mean meteorological records — of the climatic conditions in Period II. But the evidence of the pollen diagrams, coupled with that of stratigraphy, affords sufficient information. *In order to arrive at the same conclusion as* FAGERLIND's, *one has to reverse the significance of well-known facts:* it becomes necessary to consider that the dry forest species must require greater humidity, as they gradually diminish in frequency towards the said culmination of Period II (Ser. 34, 81, 84, 90, etc.).

The assertion which he wrongly ascribes to me: »the raising of the cloud belt is accompanied by a reduction in humidity, and its lowering by an increase» is a fallacious generalization of the local conditions in the higher levels of Kauai, as may be clearly seen from my Fig. 28 (SG, p. 118, reproduced in this paper, p. 34). The problem

is not as simple as FAGERLIND thinks, and his conclusion beginning »If his views are logically applied . . .» is not logically justifiable.

b. The large rhythmical changes may have occurred *per saltum*.

I have called attention to this phenomenon as an alternative (SG, p. 115), as the indications are inadequate as proofs. FAGERLIND asserts that it cannot be observed in the diagrams, but continues: »If it occurs some few times, this is entirely without significance as we do not know, of course, that the separate sample cores correspond to equally long periods of time.» What I have said is just that it occurs some few times, and — although FAGERLIND says nothing of this — I myself have stressed the limitations of the chronology. What FAGERLIND has said on this point is, in other words, a repetition of my text, coupled with an unjustified denial of a possibility. It is the more unjustified as in for instance Närke, in Sweden, from where the diagram closely agreeing with the Hawaiian standard diagram in Fig. 11 has been obtained, such rapid changes have been shown to occur, although this has been unknown to FAGERLIND.

c. The succession in the rain-forest.

FAGERLIND (p. 78—79) even ventures to deny the succession *Cheirodendron-Myrsine-Metrosideros*, which is clearly noticeable in the diagrams. He says that this is so rare in the diagrams that it can scarcely be more than fortuitous. Anybody capable of reading clear pollen diagrams would have come to a different conclusion. The collocation of diagrams republished here (p. 25–26 and p. 38, Fig. 13: 1) incontrovertibly supports my views.

d. The peculiarities of the *Cibotium* curve.

The peculiar course of the *Cibotium* curve in Diagram 81 (Fig. 6), and its partial conformity with the humification curve — humification measured in absolute numbers of pollen in each preparation —, is in my opinion best explained by the composition of the rain-forest having been affected by a series of humidity changes regularly spread over the post-Glacial warm period: short dry periods (with or without accompanying storm falls) have produced gaps in the forest, *Cibotium* has grown up, and in a few decades

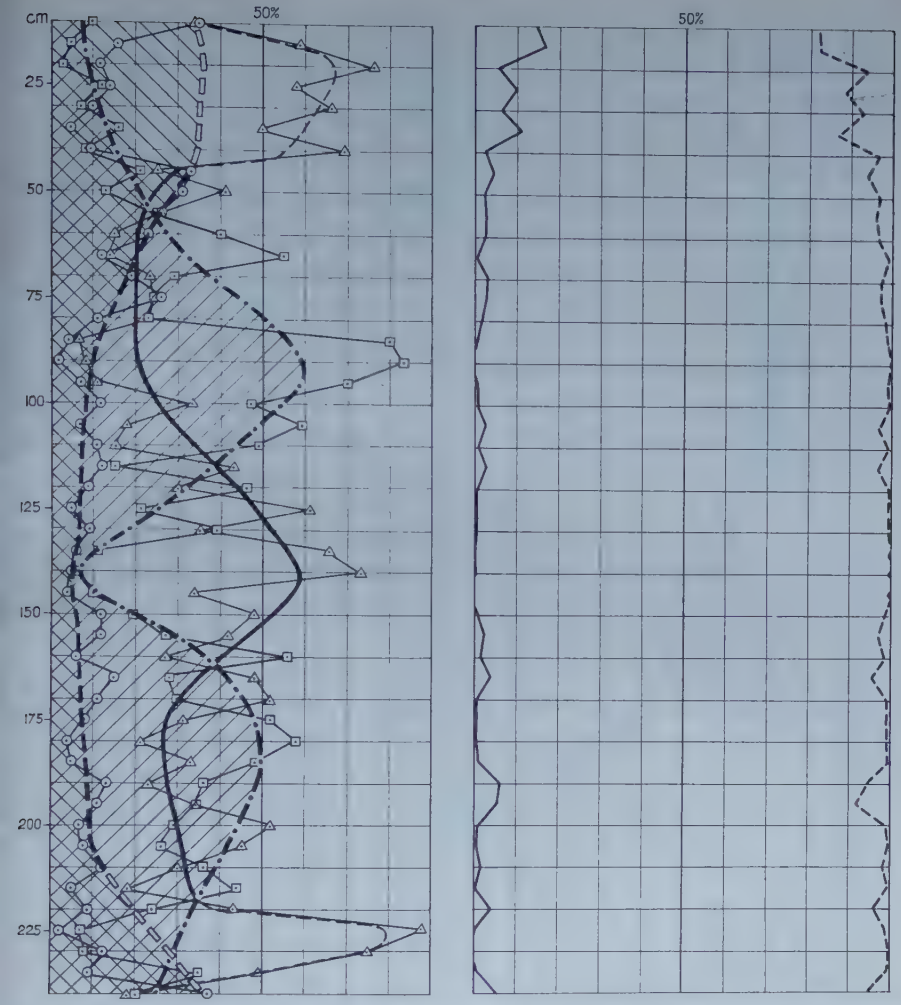

Fig. 3. Pollen diagram from Kauai: Kilohana, 1220 m elev., showing the succession of rain forest trees that has been denied by FAGERLIND. For symbols, see Fig. 4. The *Chenopodium* values (= ruled area in right diagram of Fig. 5) not specified here. *Metrosideros* culminations not belonging to Period II drawn with thin, broken lines. See also fig. 12 (p. 36). — Redrawn from SELLING 1948, Pl. 26, Diagram 81.

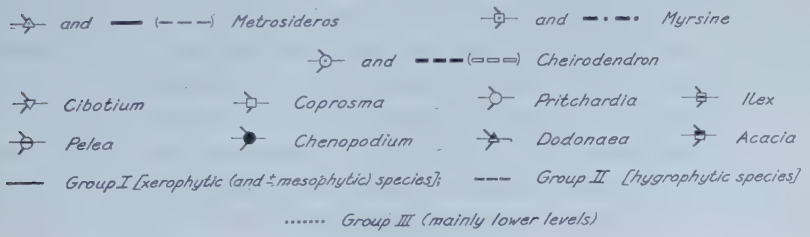

Fig. 4. Symbols for Hawaiian pollen diagrams reproduced in Figs. 3, 5, and 13 (symbols for the various genera reproduced from SELLING 1948, p. 88, Fig. 25).

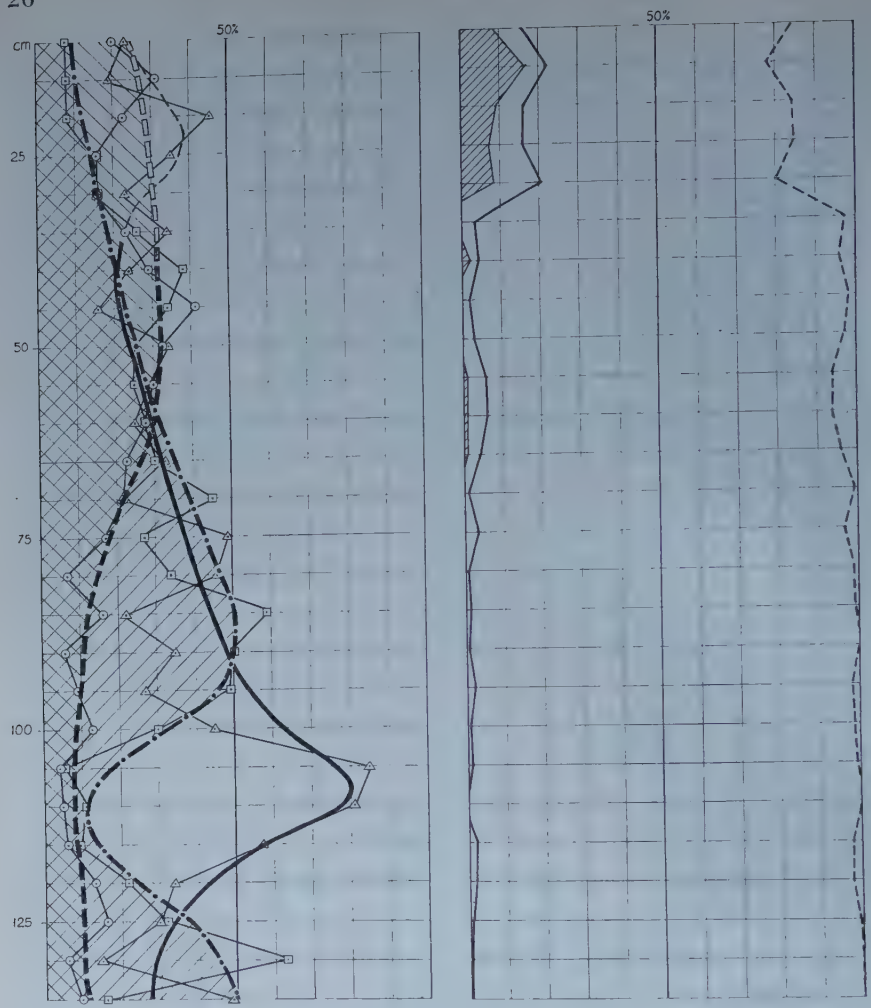

Fig. 5. Pollen diagram from Kauai: Waialeale, showing another example of the succession *Metrosideros - Myrsine - Cheirodendron*; it corresponds to the upper part of the diagram in Fig. 3. For symbols, see Fig. 4 (and Fig. 3). Ruled area in diagram to the right: *Chenopodium*. — Redrawn from SELLING 1948, Pl. 27, Diagram 90.

Metrosideros has again become dominant in the same way as in our days: by germinating in the tree fern crowns and sending down aerial roots that eventually kill its supporter. In the diagram, *Cibotium* culminations are followed by *Metrosideros* culminations. This is a common phenomenon in Hawaii, the Polynesians were already well aware of it, I myself have studied it, and persons who know the problems of tropical rain forests (for inst. Dr. C. G. G. J. VAN STEENIS)

have concurred in the explanation. FAGERLIND, who evidently does not know this forest, designates my explanation »confused and far-fetched». He says (p. 79): »it goes excellently to explain the relation of the *Cibotium* values to the humification values as well as to the *Metrosideros* and *Myrsine* values as the result of selective pollen destruction.» Without further elucidation he also asserts that »soil experts» consider fluctuations in the degree of humification not to be due so much to changes in the humidity as to changes in mineral contents. As I have throughout my series found occasional ash particles, FAGERLIND is ready with an interpretation to which he immediately gives precedence: these ash particles must of course be responsible for the destruction of the peat, and also of other pollens than those of *Cibotium*; the frequency of the tree fern component of the forest has not changed at all! So easily the problems cannot be solved, however.

In the first place it cannot be denied that even to this day there is a regionally determinable connection between peat formation and humidity, and that this connection is particularly sensitive not least in Hawaii. In these islands peat deposits cease to occur far above the levels where the precipitation has diminished to values which in for instance Scandinavia would be more than sufficient for them to form. The rôle of the volcanic ash in Hawaii is moreover quite unknown. There is furthermore not the slightest indication that it is concentrated especially to the strata in which I have found a higher degree of humification. Rather is it peculiar that I did not find the ash concentrations I was looking for in these very samples (SG, p. 51); one would have expected to find them there, as these strata have been growing at a particularly slow rate.

It is also worth asking from where this supposed ash in Sta. 81 would have come, *that did not affect the peat at Sta. 90* (see Fig. 7), *although this is but some 12 kilometres away*, and although it would have been deposited particularly heavily not once, but repeatedly (six times in all in the post-Glacial warm period). This is very remarkable. There is no crater close to Sta. 81 at Kilohana. If we consider the Koloa eruption, which has been tentatively ascribed to »late Pleistocene or early Recent times» (see quotation in SG, p. 52), its centre is nearer to Sta. 90 than to Sta. 81, and the absence of the FAGERLIND ash at Sta. 90 is equally inexplicable. There remains the possibility of the large volcanoes, on the southernmost islands, East Maui and Hawaii (Fig. 8), having had something to

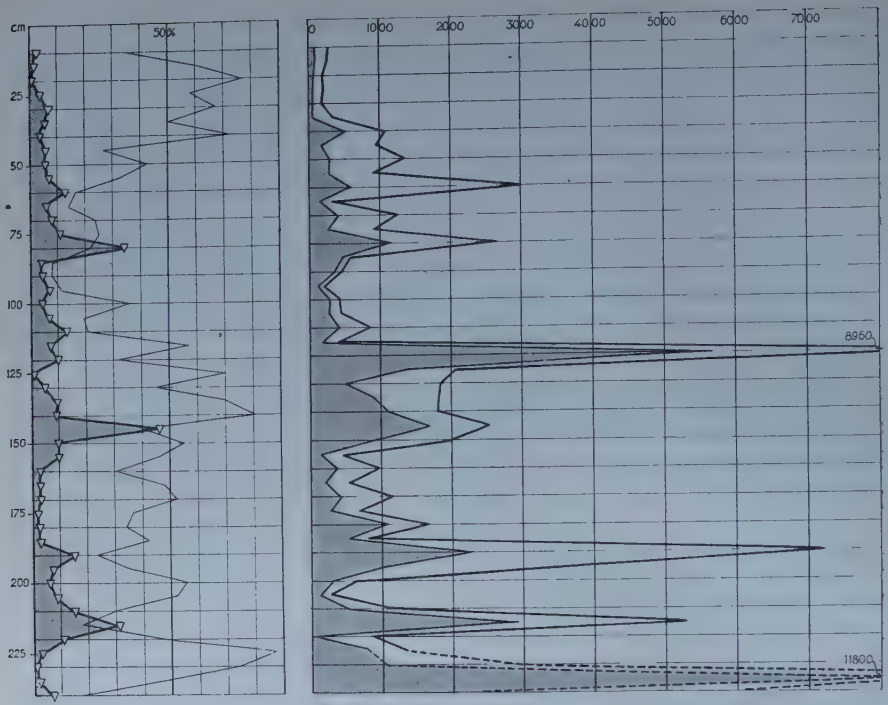

Fig. 6. Comparison between the curves for *Cibotium* (left, shaded), *Metrosideros* (left, thin line without shading), and humification (right) in Sta. 81 (Kauai: Kilohana, 1220 m elev.). Humification expressed in absolute number of pollen grains per slide (shaded part = forest tree pollens included in the diagrams; the remainder = other pollens and spores, mainly herbs and low shrubs). The *Cibotium* and *Metrosideros* curves taken from the general pollen diagram that has been made for this station. It should be noted that the highest *Cibotium* (tree fern) culminations are symmetrically arranged in relation to the maximum value, that each of them seems to correspond to the beginning of a *Metrosideros* culmination, and that they have exact counterparts in the humification curve, but that *otherwise there is no close correspondence*. Thus, there are notable differences, in 120 cm depth and at the bottom of the section in particular. These differences make FAGERLIND's attempt at explanation ill-considered. Other considerations (see the text) reveal further gaps: it is wholly unsupported by facts.
Se also Fig. 7. — Redrawn from SELLING 1948, Pl. 26, Diagram 81.

do with it. But then again one must ask: in that case, why was this phenomenon confined to Kilohana on Kauai, furthest to the north, and why does it not appear at Sta. 90 on the same island — which in such an extensive ash rain is in a quite comparable position —, nor on the intervening islands? Molokai (Sta. 1) has been analysed in particular detail (SG, Pl. 24), but no trace of it was found there.

FAGERLIND's supposition does not become any more probable if we analyse its local application with due appreciation of what act-

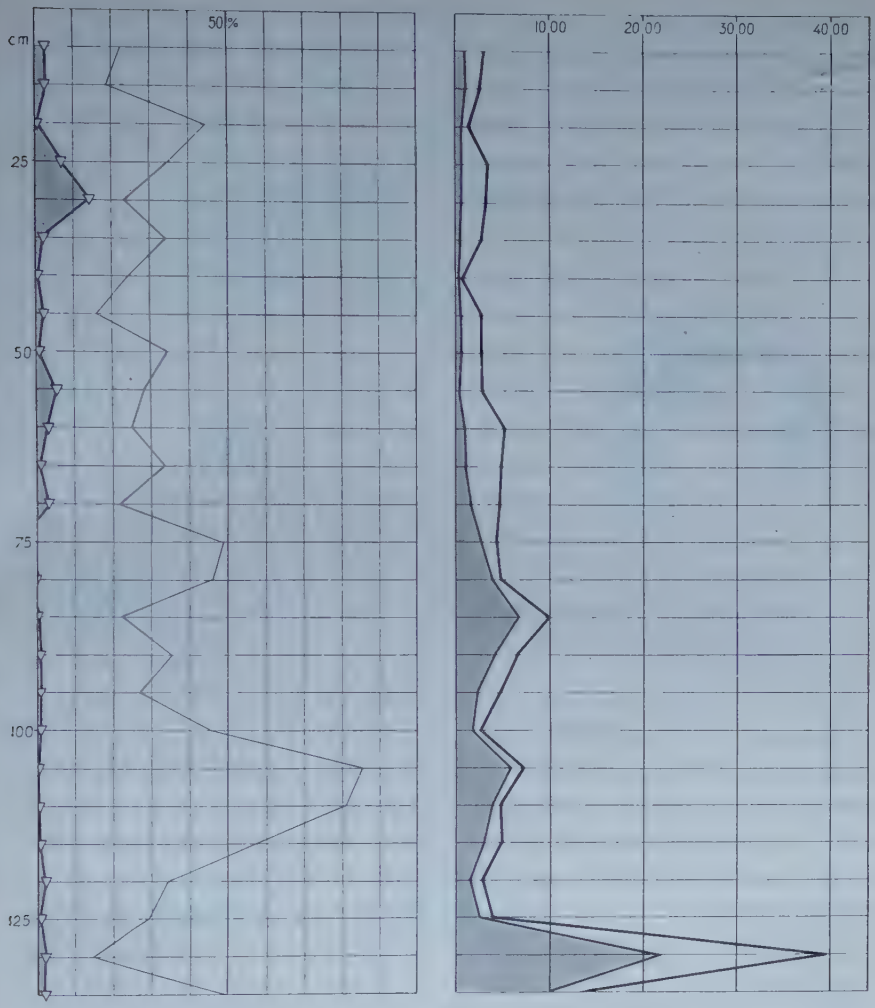

Fig. 7. The curves for *Cibotium* (left, shaded), *Metrosideros* (left, thin line without shading), and humification (right) in Sta. 90 (Kauai: Waialeale). The curves have been obtained as in Fig. 6. In this locality there is no parallelism between the two curves — not even in 130 cm depth where the humification is considerable. Nor is there anything of the characteristic variations in the *Cibotium* and humification curves to be seen in Diagram 81 (Fig. 6), although the distance between the two stations is only some 12 km. If FAGERLIND's supposition about the culminations in Diagram 81 were correct (he thinks they were caused by ash showers), one would have expected such culminations to occur here, too; there is no crater close to Sta. 81. Acc. to the present author, these differences are best explained by assuming different humidity conditions, more variable in Sta. 81 at Kilohana that here on Waialeale. — Redrawn from SELLING 1948, Pl. 27, Diagram 90.

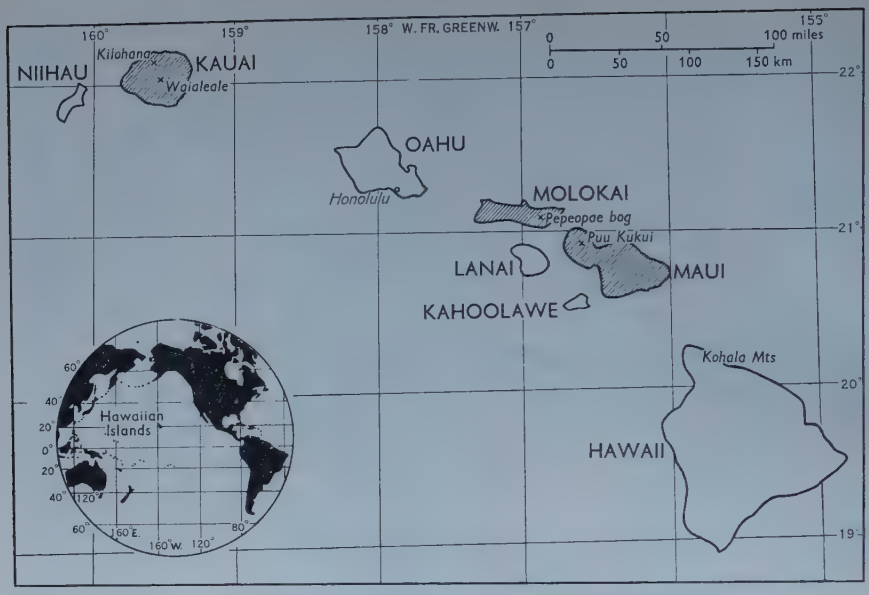

Fig. 8. Map showing the position of the author's boring stations in the Hawaiian Islands and the location of the islands from where the supposed ash showers discussed in the text could be expected. — From SELLING 1948, p. 11, Fig. 1.

ually can happen in nature. Is it even likely that the process causing a destruction of the peat which according to FAGERLIND must have gone as far as destroying most pollens and spores, can have been progressing in the mire *without affecting the surrounding rain forest*? After all, FAGERLIND is presuming far more radical changes than I find necessary for an explanation or we have any reason to expect in Period II. Incidentally, the differential destruction of which he is speaking has already been discussed and found to lack any real basis. In Fig. 6 there is very little *Cibotium* in the strata with maximum humification (120 cm and at the bottom) and in Fig. 7 there is no correspondence whatever. If FAGERLIND's supposition were correct, one would expect *Cibotium* culminations in these levels in particular. Would not a destruction as far-reaching as FAGERLIND assumes, also affect the floristic picture of the samples? That picture reflects, after all, that relative paucity which is typical of Hawaiian areas well inside the periphery of the rain forest. And above all: would not such a destruction be evident in an agglomeration of corroded pollen in the strata involved? Pollen corrosion is no sudden process. Whoever has himself made pollen analyses knows that it can very easily be seen. In these strata there is no sign of it.

I can therefore find nothing to support FAGERLIND's attempt at explanation. My interpretation is far more likely, being based on simple, well known facts of rain-forest dynamics and — in conformity with the general results of the pollen analyses — does not assume more than moderate changes of humidity in the Kilohana district. The local delimitation of the phenomenon is moreover quite naturally explained in this way. DUTTON's statement (1884, p. 88) that in the Hawaiian Islands there are »almost as many climates as there are square leagues» may here be quoted.

VII. Periods I and III.

On p. 79—80 FAGERLIND discusses the *Chenopodium* curve. Earlier (see p. 19) he had seen no reason why horizontal displacements of the border between rain forest and dry forest need be assumed. He now tentatively considers the idea, and also to some extent that of vertical displacements, but expresses himself as if my conclusion on this point were purely hypothetical (comp. the expression »If the advance . . . is really due to the pressing down of the anti-cyclonic rain belt», FD, p. 80). It is therefore of interest that LEOPOLD (1949) has by purely meteorological means shown that the inversion limit is affected in the way I have found. He writes in a letter of 24 May, 1950:

»It was particularly interesting to me that you were able to make such a logical set of assumptions on the probable changes of the inversion from your pollen data alone. This was particularly good in my opinion, because at the time of your work there was no direct indications from the upper-air data that the inversion fluctuated in any such manner as you postulated.»

The question is how far these vertical displacements have affected the peak of West Maui. That the effects have differed on West Maui and on Kauai — Molokai is to my mind indubitable.

FAGERLIND alleges that I definitely consider the summit of West Maui to have reached above the inversion limit, although I say (p. 109, the spaced-out part) »*above or in association with the inversion limit*»; I also pointed out that that limit may at the time have been more diffuse than in recent times (see SG, p. 111 and 137). Nowhere do I say that the *Chenopodium* pollen »must therefore have been produced on the present surface of the mire, or immediately adjacent to it, during a period when the rain forest had re-

treated» (Fd, top of p. 80). On the contrary, I have (p. 110—111) distinctly said that »I have, as mentioned, no proof that the species can exist on a (periodically or consistently) dry peat surface»; peat existed throughout Period III in the same places as now at the summit of West Maui. But I have said that in Period III *Chenopodium* may be assumed to have covered »a considerable portion of the open areas in the present *mire districts*, at least those of higher elevations, or in their immediate vicinity» (italics here). »Mire district» is a more comprehensive concept, which includes the whole precipitation area where mires occur in our days. Obviously, my statement does not mean that the species was hanging over the margin of the present mire at the summit — more especially as peat was forming there all the time —, and least of all has been growing on the mire itself. It is a well known fact, however, that where a mountain peak projects above the surrounding belt of trade wind clouds, these will pile up on the windward side, and leave the leeward side relatively bare (I have myself seen this phenomenon very distinctly developed on Mauna Kea and Mauna Loa, the highest peaks in the Island of Hawaii, on 29 July, 1949). I have assumed that similar conditions have obtained on the peak of West Maui at the time in question; speaking regionally, *Chenopodium* could then not have been far away, but neither could it have been in the immediate vicinity. Incidentally, I expressed myself much more cautiously than Fagerlind represents me to have done. My conclusion (Sg, p. 110) reads:

»From the peat formation it would seem indisputable that the locality has not been completely dry. Perhaps the humid patches have been ± local. One could imagine a relatively diffuse zone of frequent mountain fogs near the upper, uneven boundary of the cloud belt (see Pls. 1 and 2) in which these exposed parts have received more moisture than others; within these districts the peat formation could have continued. But at the same time it seems reasonable to assume that the moisture has not been equally distributed over the year, but that periods of drought have occurred. *Chenopodium* could thus be thought to exist, on bare rocks, etc., not far from the peat strata in question.» I again emphasize that »not far from» is not equivalent to »adjoining».

I need say no more of Fagerlind's quotations from my text. In the introduction to the present paper (p. 12–13) I pointed out that his criticism (Fd, p. 80), which was based on these quotations, includes ideas which I myself have mooted. In the cases of Maui and Kauai it is certainly a question of »varying distances», which

is exactly what I have pointed out, and I have also stressed that in Maui the vertical component must have had a stronger influence on the displacement, seeing that all the facts would not be covered if we regard the phenomenon as a merely horizontal displacement.

There now remains the question of how far *Chenopodium* has moved in this combined advance. FAGERLIND rejects the idea that the species grew at the margin of, or just outside, the present mire areas (comp. above). His motives are wholly negative. I cannot find the following conclusion (FD, p. 80) particularly binding for the present case: »If the pollen really possesses wide dispersal capacity — which I believe is correct (comp. FD, p. 74: »evident») — then that is more likely to argue in favour of dispersal from a more remote locality being possible». Dispersal capacity *per se* can hardly be regarded as evidence of the distance between the source and the place of deposit. I have not denied that part of the pollen — even a considerable part (comp. the Kauai diagrams, with values up to 33 %) — may have come great distances, but the difference between 33 % and 70—80 %, which latter value is reached in the summit area of West Maui, is after all considerable. It should also be noted that *Chenopodium* is not the only effective producer and disperser of pollen. The values 70—80 % are reached in competition with the aggregate production of all the rain-forest elements of the diagrams, including the mass producer *Metrosideros*, and moreover in localities directly facing, not the leeward side, but the large expanse of the rain forest. It does not seem reasonable to me to assume, as FAGERLIND does, that this dominance of a subalpine and leeward element is due to distant dispersal alone (see also p. 21).

VIII. The Datings.

The criticism also contains some lines on the datings, which must finally be touched upon. FAGERLIND says (p. 80): »the author

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(Continued from the next page:)

The bottom part gives a schematic representation of the tentative interpretation of the various stages in the diagrams. Shaded part: cloud belt. Ruled areas and the corresponding arrows indicate the rain-forest forming effect of the trade wind rains (thicker arrows and lines: winds more constant or more rain-bringing). The positions of the diagram localities are shown by crossed cirles. The thin arrows in A and E show the course of the trade wind rains in relation to the summits. The figure shows only the general trends deduced from the diagrams; the exact position of the limits of the cloud belt and the vertical variations of the rain fall are merely hypothetical. Conditions on the leeward sides are omitted. — Reproduced with immaterial adjustments to the original text from SELLING 1948, p. 118, Fig. 28.

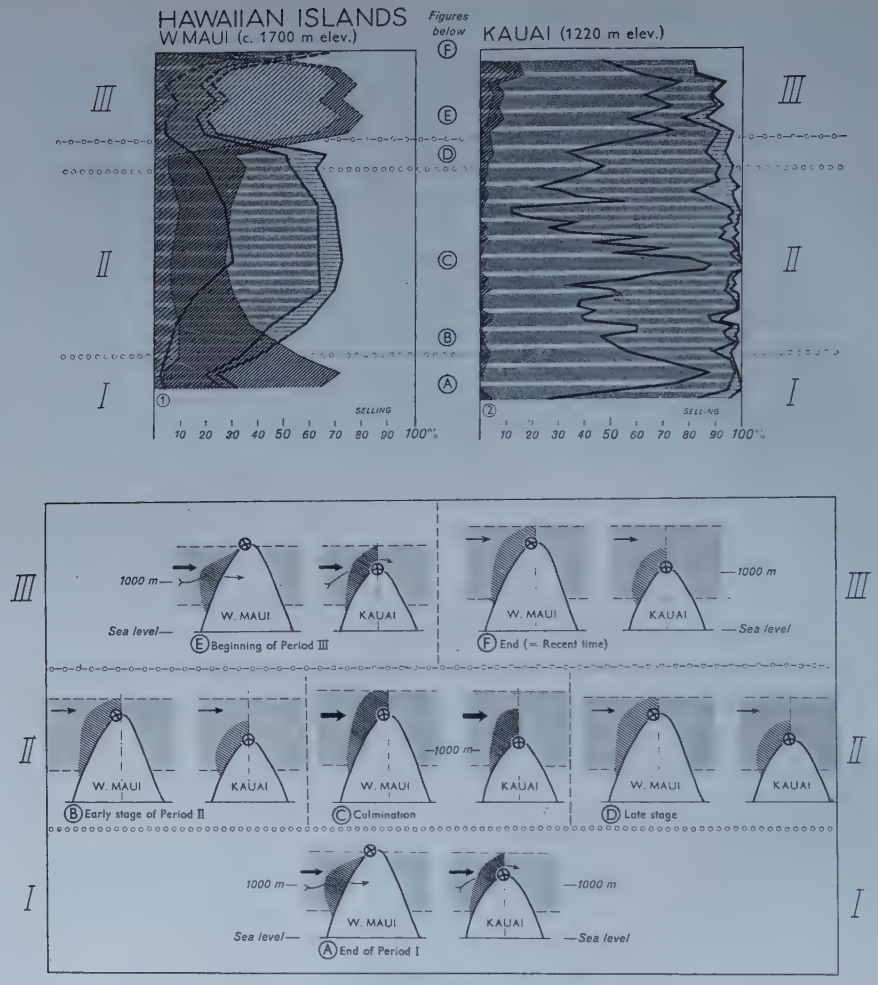

Fig. 9. The two main types of Hawaiian pollen diagrams (in SELLING 1948) and their parallelization. In the diagrams thick lines delimiting areas with horizontal bands mark mediocratic elements (thick bands: *Metrosideros* and — of minor importance — *Cibotium*, *Pelea*, and *Ilex;* medium thickness: *Myrsine* and *Cheirodendron;* thin bands: *Coprosma* and *Pritchardia*); thin lines and obliquely ruled areas: terminocratic elements (spaced oblique lines: *Chenopodium*, close do.: *Dodonaea*, *Myoporum*, *Sophora*, and *Acacia*). The diagrams provide beautiful examples of revertence and regional parallelism. The one from the 1700 m locality shows, during Periods I and III, a retreat of the rain forest, while at the 1200 m locality the rain forest species of the Period II culmination (*Metrosideros*) reappears as a dominant species also during Periods I and III, due to local meteorological conditions (comp. the bottom figure). The parallelization does not include details. The Group III curves (lower levels) have been omitted. Due to sampling conditions, the values of the 1700 m diagram represent much longer periods and are accordingly much more smoothed than those of the 1200 m diagram, which shows waves of lower orders, too.

(Continued on p. 33, bottom.)

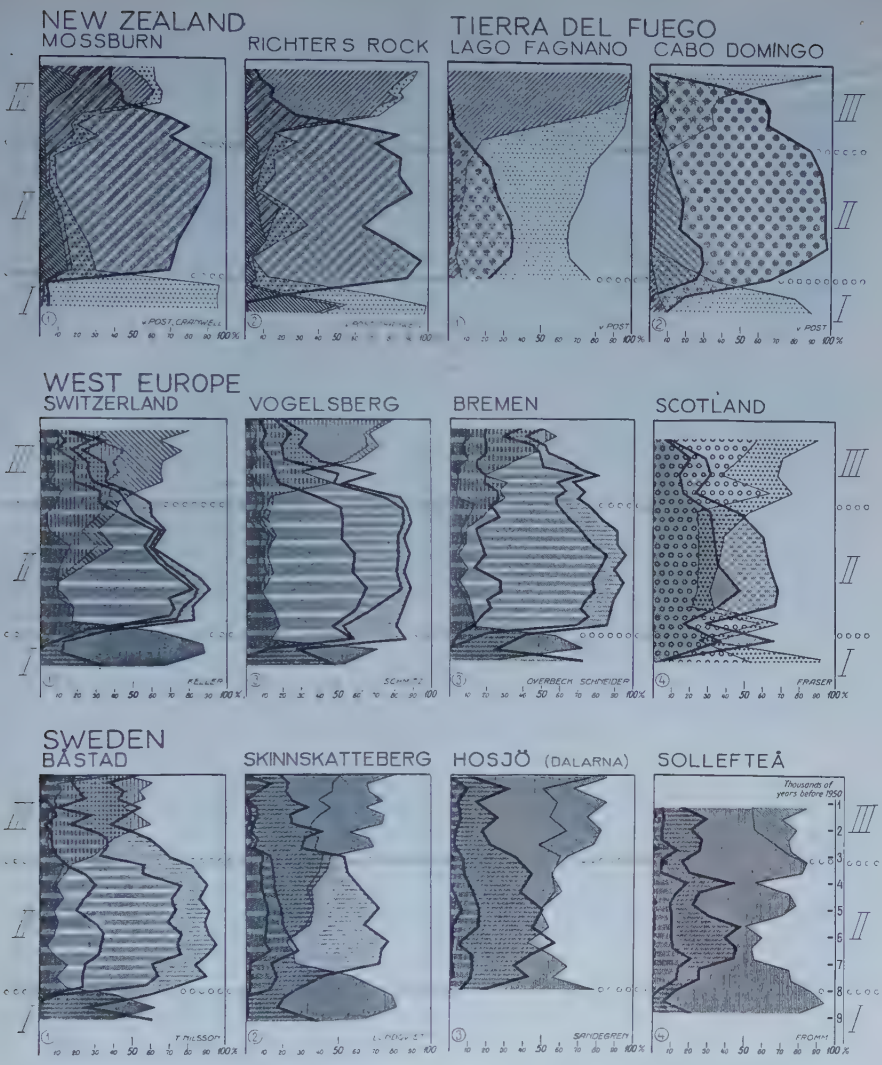

Fig. 10. Synchronized pollen diagram chains from New Zealand, Tierra del Fuego, West Europe, and Sweden, for comparison with the Hawaiian diagrams in Fig. 9. The Sollefteå diagram (geochronologically dated) has served as a vertical standard scale. Areas bordered by thick lines: mediocratic elements (in New Zealand: *Dacrydium*, *Phyllocladus*, and *Podocarpus* = lowland rain forest, in Tierra del Fuego: Caryophyllaceae and grasses, in Scotland: »wood» and hazel, in the rest of West Europe and Sweden: *Quercus* + *Tilia* + *Ulmus* = mixed oak wood, *Alnus*, and *Betula*. Areas bordered by thin lines: terminocratic elements (in New Zealand: *Metrosideros umbellata*, *Nothofagus Menziesii*, etc., and grasses + Cyperaceae, in Tierra del Fuego: *Nothofagus pumilio* + *N. antarctica* and Cyperaceae, in Scotland: *Calluna* and grasses + Cyperaceae, in the rest of West Europe and Sweden: *Pinus*, *Picea*, *Fagus* ⁘ *Carpinus*, and *Abies; Abies* not in the Swedish diagrams). For further details, see VON POST 1946. Diagrams originally published in VON POST 1946, compiled for SELLING 1948, Fig. 29 on p. 119, and here reproduced from the latter paper.

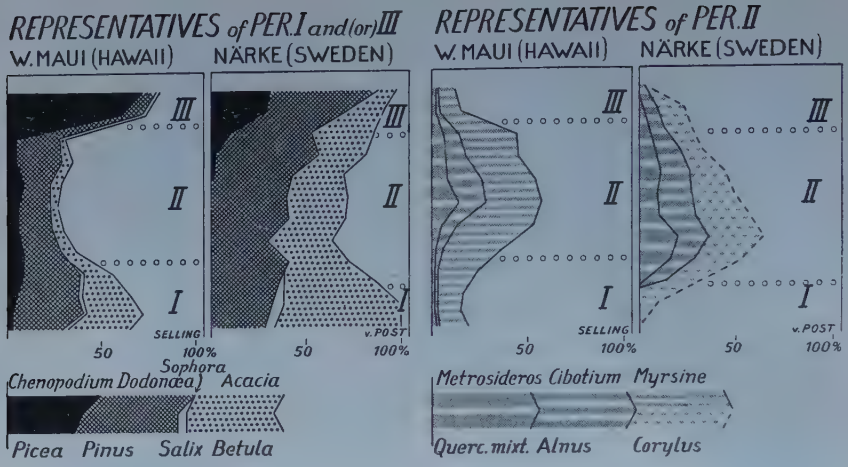

Fig. 11. Comparison between pollen diagrams from the Hawaiian Islands and Sweden. The Hawaiian diagram of 12 spectra is Diagram 34 in SELLING 1948, Pl. 24 (W. Maui, below summit, c. 1700 m elev.). The Swedish one (also of 12 spectra) is from the Nyckel Bog in Tiveden, Närke, and is one of the first diagrams by L. VON POST. Both of them only give the main features of the vegetational development during the Late Quaternary periods. No other synchronizing has been made than placing the uppermost and the lowest spectra on the same levels. The alternation between ± xerophytic (Per. I and III) and hygrophytic (Per. II) vegetation in Hawaii corresponds to ± cold-hardy and heat-requiring forms, respectively, in the temperate regions represented by the Swedish diagram. The Hawaiian section is 6 dm, the Swedish one, 6 m. —From FRIES 1949, p. 352, Fig. 1.

has tried to fix a date for the conditions prevailing in Hawaii by comparing his own diagrams with those produced by LENNART VON POST and his school». My comparisons extended to a good many other works, however, which are cited in SG, p. 117, but evidently overlooked by FAGERLIND. He makes the fallacious statement that my results are mainly based on Diagram 34, and takes the opportunity of bringing out his previously discussed assertion that this diagram is one of »the more dubious ones». That he is wrong is, as I have said, proved not only by mine (Figs. 9—10) but also by FRIES' diagrams (1949, p. 352—353; here reproduced in Figs. 11—12), which are obviously ruled by the same laws to an extent that in itself raises the evidence of the Hawaiian diagrams beyond any doubt. But FAGERLIND is not satisfied: their agreement is according to him due to »sifting» of the material (p. 80—81). His reason is that not all the species of trees are included in the diagrams, but only the phytogeographically and climatically leading species. He cannot, however, show any valid

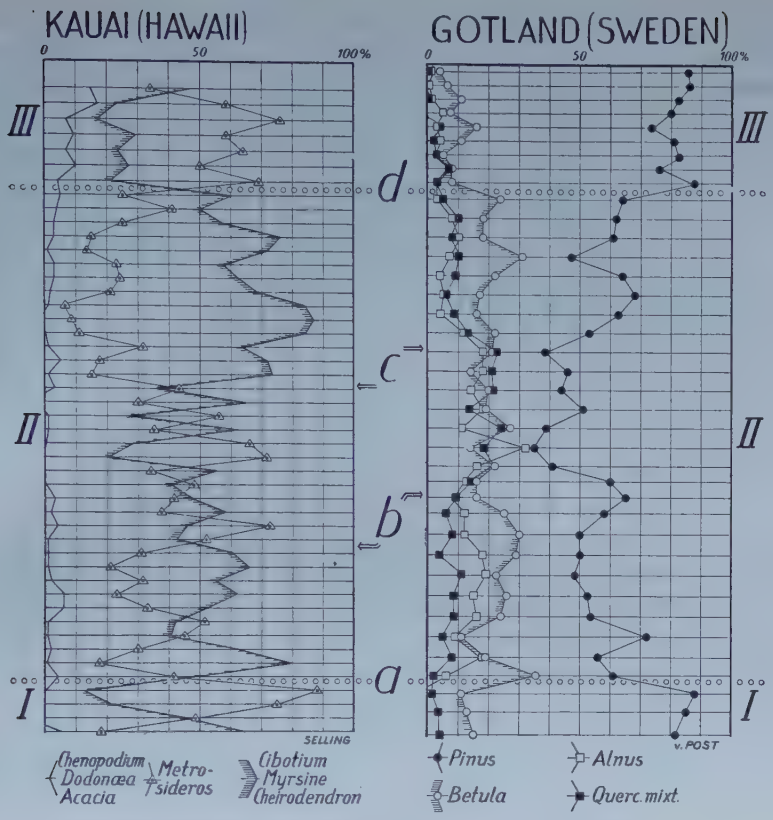

Fig. 12. Comparison between pollen diagrams from Hawaii and Sweden. The Hawaiian diagram is reproduced from SELLING 1948, Pl. 26, and is Diagram 81 from Kauai: Kilohana, 1220 m elev. The Swedish one, where, for the sake of clarity, *Picea* and *Corylus* have been excluded, is from Mästarmyr in the Island of Gotland and by L. VON POST. The diagrams are synchronized at the levels of the approximate limits between Periods I and II and between II and III. The levels of the arrows at b and c are assumed to be synchronous and delimit the culmination of Period II. The sections a—b and c—d include the remains of a transitional vegetation between this culmination of Period II and Periods I and III, respectively. — From FRIES 1949, p. 353, Fig. 2.

grounds for his suspicion, nor make any weighty objection to my selection.

The idea that the diagrams cannot be decisive unless they comprise everything, may *a priori* be deemed wrong. AUER (1933) was following that line; but that time his diagrams became indistinct, and his later arrangements are different (1941, 1946, 1950). Diagrams in papers on Tertiary deposits could also be improved by excluding immaterial pollen types. It is a well-known fact that all species are not equally decisive indicators of climate; some are

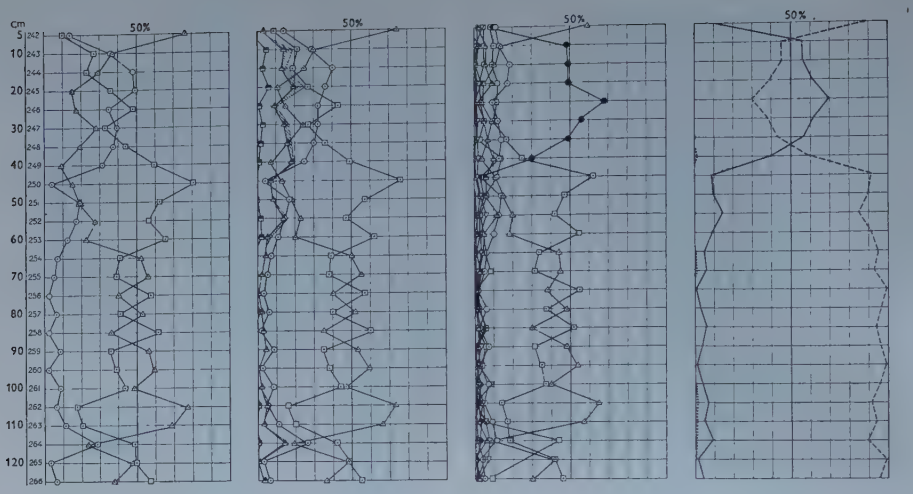

Fig. 13. Collocation of diagrams based on various parts of the material in Ser. 60 (West Maui: lowest bog; see SELLING 1948, Pl. 25, Diagr. 60). 1: *Metrosideros*, *Myrsine*, and *Cheirodendron* only. 2: *Dodonaea* and *Acacia* added (ruled area: *Acacia* added to the *Dodonaea*-curve). 3: Full set of pollen curves used in SELLING 1948. 4: Pollen curves added together into three groups: I (± xero- and mesophytic), II (± hygrophytic), III (mainly of lower levels). — It is obvious from Diagram 3 that the fundamental features in respect of rhythm have become accentuated *but not changed* by the addition of more pollen curves. Already in the diagram (1) comprising only the three leading rain forest trees, the rapid change starting above sample 250 (45 cm) is clearly noticeable. It coincides with the rise of the *Chenopodium* curve (black dots in Diagram 3), the leading dry-district indicator in Period III following the post-Glacial warm period. For symbols, see Fig. 4, p. 25.

±indifferent. To achieve comparable results in all the islands of this group, it is necessary to stick to the climatically and phytogeographically leading species. The values obtained in the pollen diagrams are moreover relative; the interrelations of but a few (in respect of the general features) ecologically distinctive types like *Chenopodium*, *Metrosideros*, *Myrsine*, and *Cheirodendron* lead to exactly the same conclusion as when they are grouped with a larger number of species (Fig. 13), and in this particular case none but relative conclusions were contemplated. The selections I have made after very thorough preparative work are well motivated ecologically; that some have been added or (like *Pelea* Type I) removed when they appeared in the actual diagrams does not affect my general conclusions. It is a procedure adopted in order to make the subject more easily surveyed. The removal of *Pelea* Type I is well motivated and easily understood from the point of view of

pollen dispersal, and also for the reason that this pollen-morphological group is with certainty heterogeneous, including as it does numerous species of varying ecological types — none of them particularly dominant. I do not think that anybody can seriously contend that the addition of *Chenopodium* is not motivated. As regards *Coprosma*, St. John's and Degener's above-mentioned observations of recent occurrences have, as expected (Sg, middle of p. 97), confirmed the validity of its inclusion. The same procedure in respect of *Pelea* Type II and *Pritchardia* makes little or no difference to the general results, but helps to illustrate the ecological positions of these groups.

Fagerlind's talk about the detailed agreement shown by the Hawaiian diagrams with diagrams from North America, New Zealand, South America, and even Europe being due to a »sifting» of my material is a negativistic argument unsupported by facts. In my papers of 1946 and 1947 he might see whether anything essential is left out; in the accounts of the material I have given, there is opportunity of checking. The necessity, in work of this kind, of proceeding as I have done will be obvious to anybody familiar with the methods of pollen statistics and conditions in the tropics. At the Botanical Congress in Stockholm in 1950 this was confirmed in a lecture by Professor P. W. Thomson, who for the purposes of analysing Tertiary pollen-bearing deposits had — independently of me — come to the same conclusion. The Hawaiian problems are in many respects the same as those met with in Tertiary pollen research.

Fagerlind ends with the following dictum: »We do not know the age of the Hawaiian peat.» He gives an alternative dating, which he thinks is a possibility showing the magnitude of the supposed difficulties. The whole paragraph need hardly be commented on. Those diagrams of von Post's (1946), which I have combined in Sg, Fig. 29 (here reproduced in Fig. 10) to elucidate the general features, are intentionally schematic. They presume an ordinary textbook knowledge of the detailed structures and extent of the periods dealt with. Moreover, the references I have given in my text of 1948 have not been inserted at random. If consulted, they would have been enough to preclude such mistakes.

Summary.

The paper is the detailed reply to FAGERLIND 1949 promised in the author's preliminary communication of the same year. It only consists of a republication of viewpoints and facts from the author's paper »On the Late Quaternary History of the Hawaiian Vegetation» (1948), with elucidating additions from other papers and personal communications bearing on the question; FAGERLIND's criticism is wholly rejected. A number of the original colour diagrams here appear for the first time in black and white.

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VERÄNDERUNGEN IN PFLANZLICHEN GEWEBEN UNTER DEM EINFLUSS MINIERENDER INSEKTEN-LARVEN.

VON

ERICH MARTIN HERING.

Als Minen bezeichnet man Frassgänge von Insektenlarven in blattgrünführenden Geweben besonders der Blätter (und der Stengelrinde) oder im Innern von Epidermiszellen, die nach aussen mindestens durch die Aussenwand der Epidermiszellen (+ deren Kutikula) abgeschlossen sind. Die in solchen Minen fressenden Larven (von denen tausende von Arten bekannt geworden sind) sind an dieses Leben im Innern von Parenchym oder von Epidermiszellen in vielfacher Hinsicht angepasst, so namentlich in den Mundwerkzeugen. Sehr spezialisierte Formen unter ihnen vermögen die Querwände niedrigster Epidermiszellen zu zerbeissen, ohne deren Aussen- und Innenwände zu beschädigen. So erzeugen sie durch ihre Frasstätigkeit Verwundungen im Innern der Pflanze, die dadurch gekennzeichnet sind, dass sie nach aussen nicht offen sind, wie es bei den meisten Verwundungen durch Insektenfrass der Fall ist. Diese Abgeschlossenheit erzeugt im Innern der Mine ein besonderes Mikroklima, dessen hoher Feuchtigkeitskoeffizient und von der Aussentemperatur abweichende Wärme kennzeichnend sind.

Wie sonst die Pflanze auf gewöhnliche Verwundungen mit der Ausbildung von Wundgewebe reagieren kann, findet man auch im Innern der Mine vielfach Wundgewebe, die von der Pflanze als Reaktion auf diese »innere Verwundung» gebildet werden. Es lässt sich erwarten, dass unter den besonderen Bedingungen im Innern der Mine, die auf dem vollständigen Abschluss nach aussen beruhen, Wundgewebe besonderer Art entwickelt werden können.

Während über die Gewebe im Innern von Cecidien eine sehr umfangreiche Literatur vorliegt, sind die Bildungen im Innern des Minenganges noch nicht im Zusammenhange behandelt worden. Da man aber die Pflanzengallen zum Teil als hochspezialisierte Minen, Minen als primitive Formen von Cecidien ansehen kann, verdienen diese Gewebeveränderungen in der Mine besondere Beachtung in Beziehung auf das Gallen-Problem. Erstmals hat Küster (1903) auf Kallusbildungen in Minen hingewiesen; später hat Schneider-Orelli (1909) sie für eine Art ausführlicher dargestellt. Eine eingehende Untersuchung über solche Bildungen bei einigen Arten finden wir bei Gertz (1918), und Hering (1926) behandelte sie im Zusammenhang mit der allgemeinen Biologie der Minierer. Später finden sich noch Einzelschilderungen bei de Meijere (1934) und Ciampolini (1949). Es folgen hier die Resultate von Untersuchungen bei einer grösseren Anzahl von Minierinsekten-Arten; bei sehr vielen von ihnen wurden Wundgewebe in den Gängen gefunden. Bei den Arten, bei denen keine Spur einer Reaktion der Pflanze festgestellt werden konnte, wird in der nachfolgenden Darstellung der Name des minierenden Insekts in ( ) angegeben. Die römischen Zahlen nach dem Pflanzennamen bezeichnen den Untersuchungsmonat. Bei Anführung früherer Feststellungen wird, um Wiederholungen zu vermeiden, auf den Autor hingewiesen.

Technik. Grundsätzlich wurden parallele Untersuchungen für jede Art an frischem und fixiertem Material unternommen. Fixierung erfolgte mit Alcoh. abs. oder nach Carnoy (6: 3: 1), nachfolgend Färbung, meist mit Safranin-Lichtgrün FS., in einigen Fällen mit Sudan III, oder mit Methylviolett 5 B und Eosin. Die Überführung in Canada-Balsam erfolgte über Nelkenöl. Frisches Material wurde erst in Wasser, dann in Glycerin untersucht. Die Schnitte wurden, je nach der untersuchten Art, in 5—15 μ Dicke angefertigt.

A. Die einzelnen Befunde.

1. *Aegopodium podagraria* L. — *Phytomyza obscurella* Fall. — Gertz (1918).

2. *Alnus incana* DC. VIII. (*Agromyza alni-betulae* Hend.) — Es ist bemerkenswert, dass hier keinerlei Reaktion der Pflanze beobachtet wird, obgleich dieselbe Insektenart in ihren Gängen an *Betula* (cf. Nr. 10) stets üppiges Kalluswachstum aufweist.

3. *Alnus glutinosa* (L.) Gärtn. V. — (*Caloptilia elongella* L.) Die Mine verläuft ausschliesslich im Innern der Epidermiszellen.

4. *id.* VII., X. — *Heliozela resplendella* Stt. — Das 1. Stadium der Mine verläuft im Medianus, oberhalb des Xylems, das auch verletzt wird; der Gang geht dann in eine Nebenrippe 1. Ordnung, von dort durch das Mesophyll zur benachbarten Rippe, im 3. Stadium dann wieder in den Medianus, dort im Grundgewebe unterhalb des Fibrovasalbündels verlaufend. Die Art hat zwei, verschiedene Reaktionen der Wirtpflanze bewirkende, Generationen. Im X. erzeugte Minen zeigen im 1. und 3. Stadium keine Wundgewebe; im 2. Stadium, bei dem einzelne schwache Leitbündel herausgefressen werden, finden sich einzelne Kalluszellen, die kaum grösser als die benachbarten Parenchymzellen sind, und die ins Lumen des Ganges ragen; auf ihren Wänden sitzen einzelne, kleine »Pektinwärzchen». Der Minenhohlraum ist infolge der in dieser Jahreszeit grösseren Menge unverdaulicher Stoffe fast vollständig mit Exkrement-Ballen gefüllt, die für Wundgewebe keinen Raum lassen. Bei den im Juli gefressenen Gängen ist das Lumen des Ganges im 1. und 3. Stadium vollständig mit Kallus gefüllt (Taf. I: 1). Zwischen den Kalluszellen werden vereinzelt Tracheen-Teile gefunden (Text-Abb. 1), bei denen es sich aber wohl nicht um umgebildete Kalluszellen handeln dürfte, vielmehr ist anzunehmen, dass sie vom zerstörtem Xylemteil abgesprengt und in den Kallus eingeschlossen wurden. Dort, wo der Gang nicht ganz von Kallus ausgefüllt wurde, konnte eine schwache Vergrösserung der Epidermiszellen beobachtet werden; ihnen anhängende einzelne Kalluszellen (Text-Abb. 2) sind wahrscheinlich aus Parenchymresten, nicht von der Epidermis gebildet worden. Die Gänge im Medianus sind vollständig mit Kallus gefüllt, der in dicht nebeneinanderliegenden Schläuchen (Taf. I: 2) in den Minenhohlraum hineinwächst und die Exkremente der Larve vor sich her zusammenschiebt. Die Kalluszellen haben hier vielfach schon einen prosenchymatischen Character (Text-Abb. 3). In der Nähe der Kotballen werden sie durch Methylviolett 5 B aussergewöhnlich intensiv tingiert. Die Epidermiszellen über solchen mit Kallus dicht gefüllten Minen erscheinen vielfach mehr langgestreckt als normal.

5. *Alnus glutinosa* (L.) Grtn. X. — (*Lithocolletis rajella* L.). — Bei allen *Lithocolletis*-Arten, die durch ihre »Faltenminen» gekennzeichnet sind, herrscht im Innern der Mine grössere Trockenheit als sonst; die Larve zieht quer durch die Mine an der Epidermis angeheftete Spinnfäden, deren Verkürzung durch Austrocknung die Faltenbildung der Epidermis bewirkt. Kallusbildung, die fast stets höhere Luftfeuchtigkeit voraussetzt, ist bei Arten dieser Gattung daher fast nie, oder nur in Spuren in den Minenwinkeln zu beobachten.

6. *Angelica silvestris* L. X. — (*Phytomyza angelicae* Kltb.).

7. *Arctium tomentosum* Mill. VII. — (*Phytomyza lappina* Gour.)

8. *Artemisia vulgaris* L. X. — (*Trypeta artemisiae* Fbr.) Die Larve durchwandert bei dieser Art immer wieder die primäre Platzmine, so dass selbst bei günstigsten Feuchtigkeit-Bedingungen Neubildungen infolge der dauernden Störungen sich nicht entwickeln können.

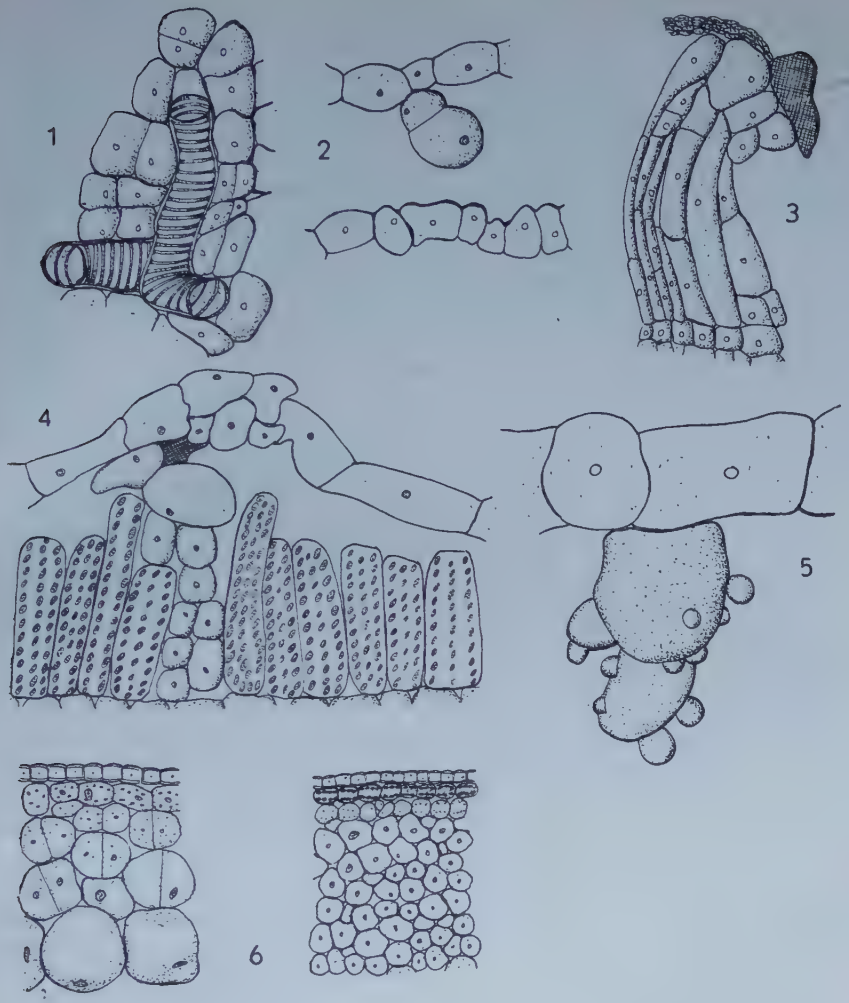

Abb. 1—6. — 1. *Alnus glutinosa* (L.) Grtn. Im Minengang von *Helizela resplendella* Hw. gebildete Kalluszellen, die Tracheen-Stücke abgedrängt haben und einschliessen. — 2. *Alnus glutinosa* (L.) Grtn. Unten normale Epidermiszellen, darüber ein Teil der Epidermis über dem Minenraum von *Heliozela resplendella* Hw. mit anhängenden isolierten Kalluszellen. — 3. *Alnus glutinosa* (L.) Grtn. Prosenchymatöse Kalluszellen aus dem Minengang von *Heliozela resplendella* Hw. drängen abgestorbene Zellen und Kot der Larve vor sich her. — 4. *Betula pendula* Roth. Teil des Minenganges von *Agromyza alni-betulae* Hd. mit Vermehrung von Epidermiszellen und ihrer Verbindung mit aus dem Schwammparenchym kommenden Kallus. — 5. *Betula pendula* Roth. Einige an der Epidermis im Minengang von *Agromyza alni-betulae* Hend. hängende Kalluszellen mit besonders grossen »Pektinwärzchen». — 6. *Crepis biennis* L. Obere Schichten eines Medianusquerschnittes rechts normal, links durch die Miniertätigkeit von *Phytomyza crepidocecis* Hering verändert, beide bei gleicher Vergrösserung.

9. *Aster tripolium* L. VIII. — *Bucculatrix maritima* Stt. Die Gänge liegen unmittelbar unter der Epidermis der Blattunterseite. Das Mesophyll entsendet in die entstandenen Hohlräume zur Ausfüllung Kalluszellen, die höchstens zweimal so gross sind wie die grössten Zellen des Grundgewebes, nur in der Längenausdehnung vergrössert sind und sich wenig vom Grundgewebe abheben (Taf. I: 7). Im engeren Hohlraum des jüngeren Stadiums erfolgt nicht eine so dichte Kallusfüllung wie im weiteren des späteren Stadiums, vielleicht im Zusammenhang damit, dass im letzten die Menge der Exkremente viel grösser ist, die vom Kallus gegen die Epidermis gedrückt werden. Die Epidermis erscheint über dem Minenhohlraum abgestorben, im noch nicht ganz mit Kallus gefüllten früheren Stadium tragen die Kalluszellen schwache »Pektinwärzchen».

10. *Betula pendula* Roth. VI, VIII, X. — *Agromyza alni-betulae* Hend. Der Minengang verläuft in der oberen Palisaden-Schicht. Über dem Hohlraum können sich die Epidermiszellen schwach vermehren (Text-Abb. 4) und wölben dadurch das Blatt an diesen Stellen. So beobachtet man sehr oft bei dieser Art starke Verkrümmungen und Verbildungen des Blattes. In den Minenhohlraum dringt, vom Schwammparenchym ausgehend, sehr reichlich Kallus ein, der sich mit der abgehobenen Epidermis verbinden kann; auch unter der oberen Palisadenschicht befindliche Palisaden können sich in der Länge strecken. Auch von ihnen können Kalluszellen abgegeben werden, die sind dann besonders klein und blass, mehr rundlich. Auch Gertz (1918) beobachtete bei dieser Art (als *albitarsis* Mg. bezeichnet) solche Bildungen.

Besonders auffällig sind hier die früher als »Pektin-Wärzchen» gedeuteten Bildungen auf der Wand der Kalluszellen (Text-Abb. 5). Sie sind hier im Verhältnis zur Kalluszelle so gross, und ihre mehrfach zu beobachtende Abrundung an der Anheftungstelle lassen es fast zweifelhaft erscheinen, ob es sich wirklich um Bildungen der Zellwand handelt, ob sie nicht vielleicht eher als Mikroorganismen anzusprechen sind, die sich auf den zarten, dünnen Wänden der Kalluszellen angesiedelt haben. Mit Safranin wie auch mit Lichtgrün tingieren sie sich sehr intensiv.

11. *Betula pendula* Roth. V. — (*Coleophora fuscedinella* Z.) Bei den Fleckminen der *Coleophora*-Arten wird stets das gesamte Mesophyll zwischen den beiden Epidermen verzehrt, und nie wird Kot in der Mine abgelagert, nie wurden Spuren von Kallus gefunden.

12. *Betula pendula* Roth. V. — (*Eriocrania rubroaurella* Haw.) Minengang zuerst interparenchymal, dann als Platz am Blattrand ausgedehnt. Das gesamte Mesophyll zwischen den beiden Epidermen wird verzehrt, nirgends erfolgt Kallusbildung, auch nicht bei Beginn am Medianusende; Verkrümmungen und Verbildungen des befallenen Blattes beruhen nur auf Austrocknungserscheinungen.

13. *Betula pendula* Roth. X. — (*Nepticula argentipedella* Z.) Das Parenchym zwischen beiden Epidermen wird verzehrt, aber an beiden bleiben noch Reste hängen. Häufig wird in der Umgebung der Mine Bildung »grüner Inseln» im herbstlich verfärbten Blatt beobachtet.

14. *Betula pendula* Roth. X. — (*Rhamphus pulicarius* Herbst). Pustelmine im Palisadenparenchym, von dem Zellreste an der Epidermis hängen bleiben.

15. *Betula pendula* Roth. VI. — *Heliozela betulae* Stt. Der Minengang verläuft im ersten Stadium im jüngsten Sprossteil, dann im Petiolus und zuletzt im Medianus des Blattes. Im Innern der Sprossachse verzehrt die Raupe fast ausschliesslich die Zellen des zentralen Markgewebes, verletzt aber auch hier und da das Xylem, und von diesen Stellen aus erfolgt eine Einwucherung von Kallus in den Minenhohlraum, der dadurch ganz ausgefüllt wird und die Exkremente zu einer zentralen einheitlichen Masse zusammenschiebt (Taf. I: 5). Man kann deutlich beobachten, dass die Kallusbildung von den radiären Markstrahlen ihren Ausgang nimmt. Manche der so gebildeten Zellenzüge weisen einen trüben, grobkörnigen Inhalt auf. Im Medianus verläuft der Gang im Grundgewebe, schneidet aber ± tief in das Fibrovasalbündel ein. Der grösste Teil des Hohlraumes wird von neugebildetem Kallus gefüllt, der von erhaltenen Teilen des Leitbündels ausgeht; er nimmt an den Markstrahlen seinen Anfang, aber die gebildeten Zellschläuche verlaufen nicht wie sonst oft in der Richtung der Markstrahlen, sondern sind umgebogen nach dem Hohlraum hin. Sie schieben den Kot nach aussen, wo er die Bildung einer Digressionszone gegen das Grundgewebe bewirkt (Taf. I: 4). Im Kallus des Medianus sind reichlich »Pektinwärzchen» auf den Zellwänden sichtbar.

16. *Betula pubescens* Ehrh. IX. — (*Nepticula confusella* Wood). Gang in den Palisaden verlaufend, anscheinend mit sehr feinem Gespinst ausgekleidet, die Exkremente in dicken Klumpen an die Epidermis gedrückt.

17. *Betula pubescens* Ehrh. VIII. — *Phylloporia bistrigella* Haw. — Der Anfang des Ganges »ringelt» Teile des Blattes und bedingt Wachstumsstörungen und Verkrümmungen des Blattes. Später wird eine grosse Platzmine erzeugt. Im Gangteil wird das gesamte Mesophyll zwischen den beiden Epidermen herausgefressen; es wächst dann ein sehr üppiger Kallus in den Minenraum hinein, der beide Epidermen herauswölbt (von denen öfters einige Zellen nekrotisch werden). Die Exkremente werden vom Kallus gegen die obere Epidermis gedrückt. In manchen Teilen des Ganges, in denen spärlicher Kallus gebildet wird, finden sich reichlich »Pektinwärzchen» auf den Zellwänden. Alle Parenchymzellen der Umgebung der Mine sind auffallend chlorophyll-verarmt.

18. *Brassica sp.* — Kallusbildung in Minen (wahrscheinlich von *Scaptomyzella flava* Fall.) cf. Küster (1903).

19. *Brassica rapa* L. em. Metzg. — *Ceutorrhynchus quadridens* Pz. cf. Günthart (1949). Die Kallus-Produktion im Medianus und Petiolus ist so stark, dass schon die Eier teilweise aus dem Eischlitz im Blatt herausgepresst wurden und dass junge Larven eingeklemmt und vernichtet wurden. (Der Eischlitz wird nach der Eiablage mit einem Sekrethäutchen vom ♀ verschlossen).

20. *Cerastium sp.* III. — (*Scaptomyzella incana* Mg.)

21. *Cirsium arvense* (L.) Sc. VII, X. — *Phytomyza affinis* Fall. — Die Mine ist ein interparenchymaler Gang: er verläuft zwischen den oberen Palisaden und dem Schwammparenchym in der 2. Palisadenschicht. Die oberen Palisaden zeigen auch an der Innenseite unverletzte Zellhäute, sind aber trotzdem chlorophyll-verarmt, was der Mine das gelbgrüne Aussehen gibt; es beruht wohl diese Eigentümlichkeit auf Unterernährung durch mangelhafte Saftzufuhr. Die Epidermis zeigt keine Veränderungen.

22. *Cistus salvifolius* L. IV. — Gangminen von *Nepticula cistivora* Peyer. — Anfänglich werden nur die Palisaden, später das gesamte Mesophyll herausgefressen. Nur wenige Schwammparenchymzellen am Rande des Hohlraumes sind hier und da vergrössert, in einem Falle wuchsen einige Kallus-Schläuche in die Lücken eines Kotballens hinein. Die obere Epidermis über und in der Umgebung der Mine ist durch Anthocyane intensiv rot gefärbt, die Färbung dehnt sich teilweise auch auf die Palisaden aus. Einzelne blossgelegte Schwammparenchym-Zellen zeigen ebenfalls »Pektinwärzchen».

23. *Clematis vitalba* L. VIII. — *Phytomyza vitalbae* Kltb. — Die Gangmine verläuft in den Palisaden, stellenweise wird auch die Epidermis soweit verzehrt, dass nur die Aussenwand stehen bleibt. Die Epidermis wölbt sich über dem Minenhohlraum sehr stark, anscheinend durch zusätzliche Zellvermehrung, und das befallene Blatt erscheint dadurch verkrümmt und verbogen, so besonders in den jüngsten Blättern. Aus dem Schwammparenchym wachsen zahlreiche sehr grosse Kalluszellen in den Minengang, stellenweise mit auffallend reichem Chlorophyllkörner-Bestand. Solche sind sehr langgestreckt und reichen bis an die obere Epidermis, so dass dieses neue Gewebe dem Palisaden-Parenchym recht ähnlich wird, wahrscheinlich auch dessen Funktionen übernimmt. Doch sind diese Zellen immer viel dicker als die normalen Palisaden. Oft tragen auch sie die »Pektinwärzchen», die am übrigen Kallus sehr reichlich auftreten, namentlich in der Nähe der Gefässbündel. Die Exkremente werden an die Epidermis gedrückt und verkleben diese häufig mit dem Kallus.

24. *Corylus avellana* L. — (*Nepticula floslactella* Haw.) cf. Gertz (1918).

25. *Crepis biennis* L. IV. — *Phytomyza crepidocecis* Hering. Die »Gallenmine» dieser Art findet sich hauptsächlich im basalen Medianus, dieser erscheint dort verdickt. Die Zellen des Grundgewebes sind hier vergrössert bis zu 240 μ Durchmesser (gegen etwa 80 μ normal) (Text-Abb. 6), der Inhalt ist anscheinend nicht verändert, nur beim Kern beobachtet man oft eine schwache Vergrösserung, oft enthält er 2 Nukleolen, wenn nicht 2 Kerne in der Zelle ausgebildet sind. Der auf diese Weise mehr fleischig gewordene Teil des Medianus wird nun von mehreren Frassgängen der Larve durchzogen. Es ist bemerkenswert, dass in diesen Gängen niemals Kallus anzutreffen ist. Das übermässige Wachstum des Grundgewebes wird begleitet von einer Vermehrung der Epidermiszellen, die ursprünglich wohl mit der Vergrösserung der Grundgewebe-Zellen Schritt hält; da aber diese infolge der sie durchziehenden Frassgänge zusammenfallen, stellen sich an der Epidermis Einfaltungs-Vorgänge ein (Text-Abb. 7). Die nor-

malen hypodermalen Assimilationszellen zeigen im vergallten Gewebe eine deutliche Chlorophyllverarmung.

Hier liegt ein Übergang von der Mine zur Galle vor, da die Larve vorwiegend das umgebildete Grundgewebe des Medianus frisst und immer wieder dorthin zurückkehrt, freilich auch Gangabzweigungen in die seitlich davon liegenden Partien des Blattes vornimmt.

26. *Dahlia variabilis* (Willd.) Desf. VII. — (*Phytomyza atricornis* Mg.)

27. *id.* IX. — *Liriomyza strigata* Mg. Der Hauptteil des Ganges folgt dem Medianus und verzweigt sich längs der Nebenrippen und ausserhalb von ihnen. Die Larve verzehrt vorwiegend Teile des Grundgewebes und auch Assimilations-Parenchym in der Nähe des Medianus. Die Leitbündel werden nicht angegriffen. An der Stelle herausgefressener Palisaden finden sich spärlich Kalluszellen, die nur wenig grösser als die des Grundgewebes im Medianus sind. Bei im VII. angelegten Minen findet sich auch in grösserer Entfernung von den Rippen oft dichter Kallus, der dicht gedrängt die Stelle der Palisaden einnimmt und gut ausgebildete Chlorophyllkörner besitzt. In der Nachbarschaft von Leitbündeln, von denen dann langgestreckte Kallus-Schläuche ausgehen, sind die Zellen ± stark zusammengepresst.

Bemerkenswert ist, dass bei der vorigen Art trotz ihres früheren Auftretens keine Kallusbildung festgestellt werden konnte.

28. *Dianthus caryophyllus* Mnch. — *Pseudonapomyza dianthicola* Vent. — Gang nur in den Palisadenzellen, dort Kallus, der die Schädigungen nicht beseitigen kann, cf. Ciampolini (1949).

29. *Fraxinus excelsior* L. VII. — (*Gracilaria syringella* F.)

30. *Glyceria maxima* (Hartm.) Holmb. III. — *Schoenobius forficellus* Tnbg.).

31. *Helleborus viridis* L. XII. — *Phytomyza hellebori* Kltb. In der Gangmine ist der untere Teil der langgestreckten Palisaden verzehrt worden, der stehengebliebene obere Teil ist nekrotisch geworden, braun verfärbt. Der Gang ist gegen das Schwammparenchym durch eine nekrotische, mit Exkrementen verschmierte Digressionszone abgeschlossen, durch die kein Kallus hindurchgedrungen ist.

32. *Heracleum sphondylium* L. VII. — *Phytomyza spondylii* R. D. Der im Palisaden-Parenchym verlaufende Gang ist arm an Kallus, der vorwiegend zwischen den Kotballen einige grosse, rundliche Zellen ausgebildet hat. Reichlicher ist er dort entwickelt, wo der Gang an ein Leitbündel stösst. An einer Stelle wurden an der Hohlraum-Grenze umgebildete Palisaden gefunden, die etwas chlorophyllverarmt und von unregelmässiger Kontur waren (Text-Abb. 8).

33. *id.* VII. — *Phytomyza heracleana* Hering. Die Platzmine ist hier interparenchymal: die Palisaden sind unverletzt. vom Schwammparenchym bleiben an der unteren Epidermis 1—3 Zellagen stehen, zwischen diesen beiden Parenchymschichten frisst die Larve. Auf den Schwammparenchymresten finden sich einige isolierte, rundliche Kalluszellen.

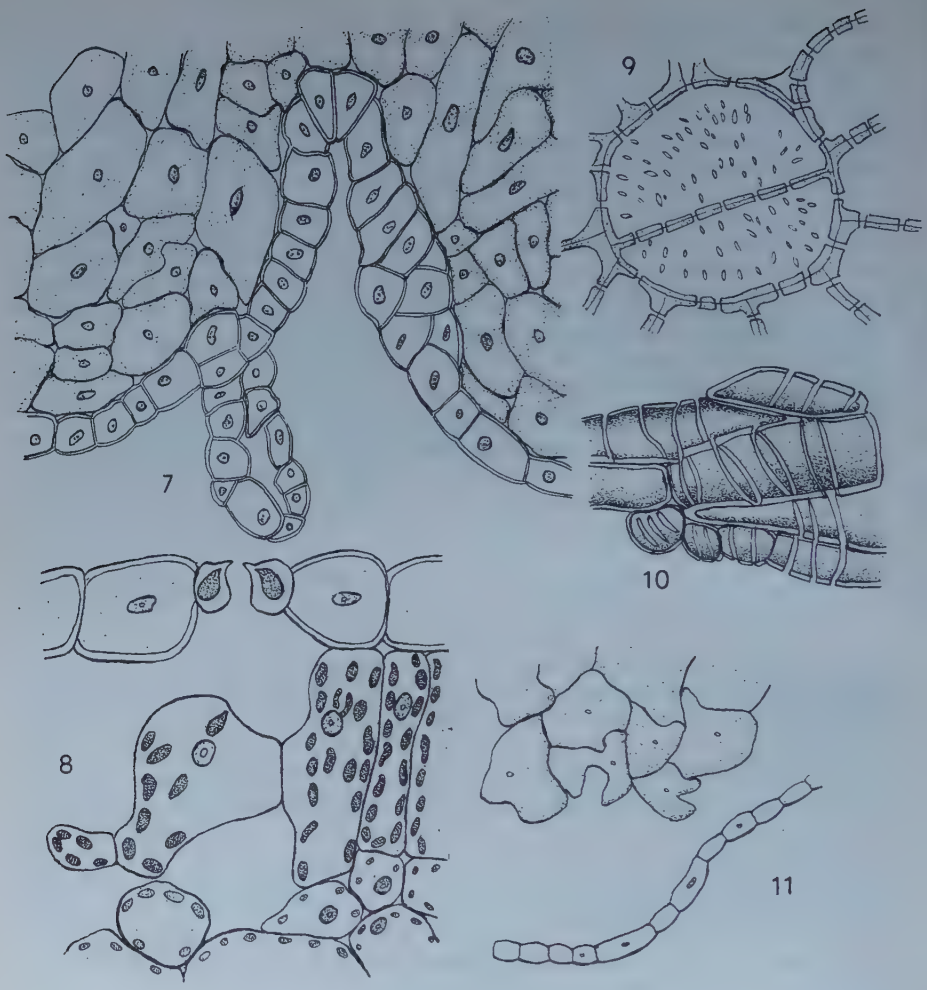

Abb. 7—11. — 7. *Crepis biennis* L. Faltenbildung der Epidermis über dem durch die Mine von *Phytomyza crepidocecis* Her. veränderten Medianus. — 8. *Heracleum sphondylium* L. Umgewandelte Palisadenzellen aus dem Minenraum von *Phytomyza spondylii* R. D. — 9. *Ilex aquifolium* L. Stark getüpfelte Kalluszellen aus dem Gang im Xylem des Medianus von *Phytomyza ilicis* Curtis. — 10. *Ilex aquifolium* L. Stark getüpfelter Kallus in der Mine (nahe der Eiablage) von *Phytomyza ilicis* Curt. im Grundgewebe des Medianus. — 11. *Phaseolus vulgaris* L. Gezipfelte Kallus-Zellen im Schwammparenchym im Minengang von *Liriomyza strigata* Mg.

34. *Hieracium lachenalii* Gmel. VI. — *Cystiphora hieracii* F. Lw. Kleine, rundliche, violett verfärbte Pusteln, bei denen die untere Epidermis herausgewölbt ist. Die 4—5 Lagen von Schwammparenchym sind unverletzt, nur an einigen Stellen sind offenbar Löcher hineingefressen. An der Grenze des Minen-Hohlraumes sind die Zellen mässig verdickt, höchstens auf das

dreifache vergrössert, solche werden wohl von der Larve verzehrt. Der Chromatophorengehalt ist unverändert. Hier liegt ein Übergang von der Mine zur Galle vor.

35. *Holcus lanatus* L. IV. — *Cerodonta denticornis* Pz. In dem feinen Anfangsgang bleiben an oberer und unterer Epidermis Parenchymzellen stehen. Von dieser interparenchymalen Mine frisst die Larve stellenweise bis an die Epidermis heran. Kallus fehlt fast vollständig, auch in der Nähe von angefressenen Gefässbündeln, nur einige Zellen zwischen den Kotballen sichtbar.

36. *Hydrocharis morsus-ranae* L. VIII. — (*Hydrellia hydrocharitis* Hering). Die obere Parenchymschicht ist verzehrt, die Epidermis sinkt herab und verklebt mit dem Schwammparenchym.

37. *Ilex aquifolium* L. V., XII. — *Phytomyza ilicis* Curt. Nach der Eiablage am Medianus (im Herbst) frisst sich die Larve in dessen Xylem hinein, in dem sie eine längere Strecke miniert; dann verlässt die Larve das Leitbündel, frisst noch eine kurze Strecke im Grundgewebe und erzeugt schliesslich im Frühjahr eine Platzmine im Palisadenparenchym des Blattes. Von den 3—4 Palisaden-Schichten bleibt die oberste stehen, die übrigen werden verzehrt, wobei oben und unten im Platz Reste der Zellen stehen bleiben, die nekrotisch werden und oft mit Kot imprägniert sind. Dort wurde kein Kallus beobachtet, doch hat ihn Küster (1925) in grosser Mächtigkeit festgestellt und sogar Verwachsung der Kallusfäden mit der Epidermis beobachtet. In dem zum Platz führenden Gang im Grundgewebe des Medianus, in dem auch Teile der Sklerenchymscheide verzehrt werden, findet sich nur selten einmal eine Kalluszelle. An der Eiablagestelle ist die Epidermis gesprengt; darunter liegen abgestorbene Zellen, die von üppig ins Innere strahlenden Kallus abgedrängt wurden. Diese Zellen sind infolge starken Druckes ganz abgeflacht. Gleichartige finden sich auch dort, wo der Gang das Phloem durchbricht. Im Xylem ist der Gang vollständig von dicht aneinander liegenden, stark verdickten Zellen gefüllt, die zahlreiche schlitzförmige Tüpfel (Text-Abb. 9) sehr deutlich erkennen lassen. Die Tüpfel der ältesten Stellen sind zuweilen ausgesprochen ringförmig (Text-Abb. 10), wodurch die Kalluszellen hier eine tracheale Umbildung erfahren haben. Innerhalb des kallusgefüllten Ganges im Xylem ist eine Digressionszone sichtbar, aber auch ausserhalb von ihr findet sich noch Kallus (Taf. I: 3); in der Nähe der Eiablagestelle ist sie noch wenig deutlich.

Es ist eine seltene Erscheinung, dass eine Mine im Innern des Xylems verläuft, damit im Zusammenhange steht wohl auch die Andersartigkeit der Kallusbildungen.

38. *Impatiens parviflora* DC. IX. — (*Liriomyza impatientis* Brischke, Gang in den Palisaden).

39. *Kleinia neriifolia* Haw. V. — *Liriomyza kleiniae* Hering. Gangmine zuerst im Schwammparenchym, kann bis an die untere Epidermis heranstossen. Wo eine Verletzung des Medianus nicht erfolgt ist, finden sich

keine oder nur wenige Kalluszellen. Wo die Leitbündel des Medianus verletzt wurden, wächst von der Unterseite eine dichte Schicht von Kallus-Schläuchen in den Hohlraum hinein, abgestorbene Zellreste und Exkremente vor sich her schiebend. Diese Zellen haben meist schon einen etwas prosenchymatischen Character angenommen (Taf. I: 9).

40. *Laburnum anagyroides* Med. IX. - *Phytomyza cytisi* Brischke. Die Gangmine verläuft zuerst im Schwammparenchym, wobei Palisaden und eine Schicht des Schwammparenchyms an der unteren Epidermis stehen bleiben. Dort werden einzelne Kalluszellen aus dem Schwammparenchym (nicht aus Leitbündelscheiden) gebildet. Später verläuft der Gang dann in den Palisaden und enthält keinen Kallus mehr.

41. *Lamium album* L. — (*Liriomyza strigata* Mg., verosimiliter). cf. Gertz (1918).

42. *Lonicera periclymenum* L. und
43. *L. xylosteum* L. — *Phytagromyza xylostei* R. D. — cf. Gertz (1918) (als *Phytomyza lonicerae* Brischke).

44. *Luzula pilosa* (L.) Willd. V. — (*Dizygomyza bimaculata* Mg.). Gangmine interparenchymal, eine Schicht der kleinen, runden Palisaden bleibt stehen. Die untere Epidermis löst sich mit einer anhaftenden Schicht Parenchym oft natürlich ab, wodurch grosse Hohlräume entstehen.
45. *id.* V. — (*Phytomyza luzulae* Hering). Gangmine nur in der oberen Palisadenschicht verlaufend.
46. *id.* V. — (*Elachista geminatella* H. S.) Im 1. Stadium Mine im oberen Palisadenparenchym, auch Epidermiszellen (ausgenommen deren Aussenwand) werden verzehrt. Später wird das gesamte Mesophyll herausgefressen.

47. *Malus silvestris* Mill. VII. — *Lyonetia clerkella* L. Gang zuerst in den Palisaden, später das ganze Mesophyll einnehmend. Einzelne Zellen wie auch ganze Kallus-Schläuche sind reichlich zu finden, besonders in der Nähe der Leitbündel. cf. Schneider-Orelli (1909).
48. *id.* VIII. — *Phytomyza heringiana* Hend. Platz interparenchymal in der 2. Palisadenschicht, stellenweise Vorstösse auch durch die obere bis an die Epidermis, an solchen Stellen einzelne Kalluszellen.

49. *Nepenthes tobaica* Dans. — (*Phyllocnistis nepenthae* Hering), Gänge nur in der oberen Epidermis der Kannen, ohne irgendwelche Veränderungen.

50. *Pancratium maritimum* L. — (*Brythis pancratii* Cyr.). Gang unter der Epiderm des Blütenschaftes im Grundgewebe und Rindenparenchym, auch einige Epiderm-Zellen (ausgenommen ihre Aussenwand) werden verzehrt. Nirgends Kallus, auch nicht bei Anschnitt von Fibrovasalbündeln.

51. *Pastinaca sativa* L. X. — (*Phytomyza pastinacae* Hend., Gang in den Palisaden).

52. *Poa compressa* L. VI. — *Dizygomyza pygmaea* Mg. Platzmine im oberseitigen Parenchym, stellenweise interparenchymal. Nur einmal wurde

unmittelbar am Leitbündel ein an der Epidermis liegendes Kotkorn von einer Gruppe von Kalluszellen dicht umschlossen gefunden. Selten fanden sich 1—2 Kalluszellen im Minenwinkel.

53. *Phaseolus vulgaris* L. VIII. — *Liriomyza strigata* Mg. Bei dieser Insektenart, deren Mine sich besonders an die Blattrippen anlehnt, wird besonders häufig Kallusbildung beobachtet (vergl. Nr. 27). Dort, wo die Mine im Schwammparenchym verläuft, werden auch hier reichliche Kalluszellen gefunden; die Palisadenzellen darüber oft nekrotisch. Die Kalluszellen wiesen hier zuweilen dort, wo sie an den Minenhohlraum grenzten, eine eigentümlich gezipfelte Form auf (Text-Abb. 11). »Pektinwärzchen», durch Safranin intensiv rot gefärbt, sind reichlich festgestellt worden.

54. *Phragmites communis* Trin. — (*Elachista cerusella* Hbn.). Mine oberseitig oder das gesamte Mesophyll einnehmend, oft bleibt eine Zellschicht an einer der beiden Epidermen stehen.

55. *Pinus silvestris* L. III. — (*Ocnerostoma piniariella* Z.). Der grösste Teil des Gewebes zwischen den Epidermen ist verzehrt worden, einige Harzgänge und ihre Umgebung sind stehen geblieben.

56. *Polygonum lapathifolium* L. X. — *Euspilapteryx phasianipennella* Hbn. Die Raupe frisst im 1. Stadium im Schwammparenchym, dessen unterste Zellen stehen bleiben, aber nekrotisch werden. Das 2. Stadium liegt in der 2. Palisadenschicht, die Zellen der obersten Schicht werden angebissen und ausgeschlürft, erscheinen dann bräunlich-nekrotisch. Bei beiden Stadien finden sich wenige rundliche Kalluszellen, vom Schwammparenchym kommend, mit »Pektinwärzchen».

57. *Populus italica* L. X. — *Nepticula hannoverella* Glitz. Die Raupe lebt in »grüner Insel» im herbstlich verfärbten, abgefallenen Blatt. Der Anfangsgang befindet sich im etwas sich verdickenden Blattstiel, in dem das Grundgewebe verzehrt wird. Er ist zu einem grossen Teile mit Kot gefüllt; in den übrig bleibenden Hohlräumen finden sich einige Kalluszellen. Auf der Seite des Petiolus, die den Gang enthält, sind die Grundgewebe-Zellen etwas vergrössert und bedingen die einseitige Verdickung des Blattstieles. Dort, wo das Fibrovasalbündel mit angegriffen wird, erfolgt üppiges Kallus-Wachstum; er bildet sich auch dort schon, wo nur die Sklerenchymscheide verletzt worden ist. Von dem Kallus wird dann der Kot im Zentrum der Bildung zusammengeschoben; man beobachtet auch, dass Teile des Sklerenchym-Ringes des betreffenden Bündels abgesprengt und nach der Mitte des Kallus abgedrängt werden (Taf. I: Fig. 6). Wo innerhalb des Sklerenchymringes nicht nur Grundgewebe, sondern auch Markstrahlen verletzt wurden, bilden sich lange und zahlreiche Kallusschläuche, die in den Minenraum hineinwachsen. Bei Ausfüllung sind die einzelnen Zellen infolge des starken Druckes abgeflacht und klein. Öfters finden sich auch Digressionszonen, bestehend aus nekrotisch gewordenen Zellen, die mit Kot imprägniert wurden und bräunlich erscheinen.

58. *Populus alba* L. X. — *Nepticula turbidella* Hs. und

59. *Populus tremula* L. X. — *Nepticula argyropeza* Z. zeigen die gleichen Verhältnisse.

60. *Populus nigra* L. V. — (*Phyllocnistis suffusella* Z.) Gang nur im Innern der Epidermiszellen, deren Querwände zerbissen werden. Keine Veränderungen.

61. *Populus tremula* L. VIII. — *Lithocolletis tremulae* Z. Faltenmine im Schwammparenchym, dessen untere Lage nicht mit verzehrt wird, stellenweise werden die Palisaden bis zur oberen Epiderm gefressen. Kein Kallus (vergl. Nr. 5). Die abgehobene Epidermis über dem Minenraum enthält meistens Anthocyan.

62. *Prunus virginiana* L. VII., X. — *Lyonetia clerkella* L. Der Gang nimmt das ganze Mesophyll zwischen den beiden Epidermen ein, er ist vollständig mit Kallus gefüllt, der die Exkremente zentral zusammenpresst. Vielfach, namentlich in der Nähe von Leitbündeln, ist die Kallus-Produktion so stark, dass beide Epidermen nach aussen herausgepresst werden (Taf. I: 8). Bemerkenswert dabei ist, dass dann die Kalluszellen nicht wie sonst meistens abgeflacht sind, sondern ihre rundliche Form beibehalten haben, ein Zeichen dafür, dass der in ihnen herrschende Turgor stärker ist als der die Epidermen herauswölbende Kallusdruck. Auch hier sehr oft Digressionszonen aus nekrotischen, mit Kot imprägnierten Zellen, die den Minengang gegen das gesunde Gewebe abgrenzen.

63. *Prunus cerasus* L. VII. — *Lyonetia clerkella* L. Ähnliche Verhältnisse.

64. *Prunus mahaleb* L. VI. — *Lyonetia clerkella* L. Frassraum wie bei den vorigen ausgefüllt, auch die Zellen der hier harten Epiderm vielfach angebissen. Die Kallus-Ausbildung ist spärlicher, nur an Verletzungsstellen von Rippen stärker ausgeprägt, die Zellen rund, mit manchmal besonders grossen »Pektinwärzchen».

65. *Prunus domestica* L. IX. — (*Recurvaria nanella* Hbn.). Die Gangmine hat das gesamte Mesophyll eingenommen, nur an der unteren Epidermis Parenchymreste. Der ganze Hohlraum ist mit Gespinst ausgekleidet, Kallus-Entwicklung nicht möglich.

66. *Quercus robur* L. VIII. — *Rhynchaenus quercus* L. Der Anfangsgang liegt im Medianus, ein grosser Teil des Leitbündels mit Ausnahme des Xylems ist mit verzehrt worden. Der Hohlraum wird vollständig von Kallus ausgefüllt, der sowohl von den Markstrahlen wie auch von prismatischen Zellen des Grundgewebes seinen Ausgang nimmt, zuerst in Form von langen Schläuchen. In der späteren Mine ausserhalb der Blattrippen ist kein Kallus mehr zu finden.

67. *id.* IX. — *Nepticula samiatella* Z. Die Gangmine lehnt sich nicht an Blattrippen an, zuerst im Palisadenparenchym, dort wachsen aus dem Schwammparenchym (auch in Entfernung von Leitbündeln) einzelne grössere Kalluszellen in den Hohlraum. Auch die Epidermis wird teilweise angefressen, so dass nur ihre Aussenwand erhalten bleibt, sie erscheint überall über dem Minenraum nekrotisch.

68. *Quercus petraea* (Mattusch.) Liebl. IX. — *Nepticula albifasciella* Hein. Der Anfangsgang zieht neben einer Seitenrippe 1. Ordnung entlang, verläuft zuerst im Schwammparenchym, dann werden auch Palisaden und Hypodermzellen über dem Medianus gefressen. Der Gang ist (trotz des späten Auftretens!) ganz mit grosszelligem Kallus gefüllt, der die Exkremente zusammendrückt, und durch reichliche »Pektinwärzchen» gekennzeichnet.

69. *Ranunculus repens* L. XII. — (*Phytomyza ranunculi* Schrk.) Gang unmittelbar unter der Epidermis in den Palisaden oder im Schwammparenchym. Auch Gertz (1918) fand bei dieser Art keinen Kallus.

70. *Rhamnus frangula* L. X. — *Bucculatrix frangulella* Goeze. Die anfängliche Gangspirale zeigt, dass alles Mesophyll zwischen den Epidermen verzehrt worden ist, auch die obere Epiderm (ohne deren Aussenwände) ist angebissen worden; an der unteren hängen Reste von Schwammparenchym. Kallus fehlt. Die ganze Umgebung der Mine wie auch die Querwände der Spirale sind violettbraun verfärbt, beruhend auf dem Zusammenwirken von Anthocyanen mit der bräunlichen Nekrosefarbe der abgestorbenen Zellen.

71. *Rumex acetosa* L. IV. — (*Mantura subobtusata* Janss.) Gang in den unteren Palisaden, die oberen werden angebissen und teilweise ausgeschlürft, wodurch diese Minenanfänge gelblichgrün erscheinen. Später wird alles Parenchym zwischen den Epidermen verzehrt.

72. *Salix pentandra* L. X. — (*Phytagromyza tridentata* Lw.). Der Gang verläuft in den unteren Palisaden, die oberen werden angebissen und teilweise entleert, wodurch die Mine die charakteristische gelbgrüne Farbe erhält.

73. *Salix purpurea* L. XII. — *Phyllocnistis saligna* Z. Der Minengang verläuft ausschliesslich im Innern von Epidermiszellen, beginnt kurz in einem Blatt, verläuft durch die Epidermis des jüngsten Sprossteiles und endet in einem anderen Blatt. Die Querwände der Epidermiszellen werden durchgebissen, es dringt Luft ein, und die Aussenwand der Epidermis hebt sich ab. Dort, wo die Mine in der Zweigepidermis verläuft, ist die innere Wand der Epidermiszellen degeneriert. Die darunter liegenden subepidermalen Schichten haben mehrere Schichten Kallus gebildet, der infolge des Abschlusses durch die darunter befindliche stark kutinisierte Schicht vertrocknet und bald abgestorben ist (Text-Abb. 12). Die nächste subepidermale Schicht hat keinen Kork geliefert, sondern nur eine stark kutinisierte Schicht, so dass die Sekundärlamelle der Aussenwand dieser Zellen eine ganz ähnliche Ausbildung erfahren hat wie die der ursprünglichen Epidermiszellen-Aussenwand. Sie zeigt die gleiche lebhaft rote Färbung im Leben, tingiert sich mit Sudan III (wie auch mit Safranin) ebenso lebhaft und widersteht wie diese der Behandlung mit konzentrierter Schwefelsäure, die sonst den ganzen Schnitt zerstört. Es hat sich also unterhalb des abgestorbenen Kallus eine Zellschicht gebildet, die morphologisch wie auch funktionell der echten Epidermis gleichwertig zu sein

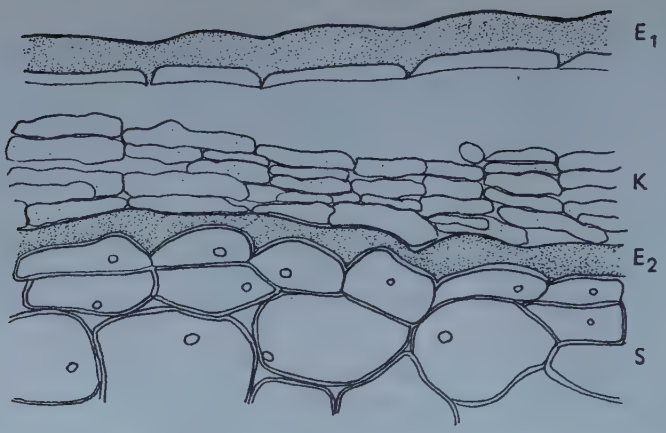

Abb. 12. *Salix purpurea* L. Teil eines Querschnittes durch die Sprossachse mit der epidermalen Mine von *Phyllocnistis saligna* Z. (E_1 = Aussenwand der Epidermis, K = abgestorbener Kallus, E_2 subepidermale Zellenschicht mit stark kutinisierter Aussenwand, als Epidermis fungierend, S = subepidermales Parenchym).

scheint (eine Abgrenzung der kutinisierten Sekundärlamelle gegen die eigentliche Kutikula war hier wie auch bei der echten Epidermis nicht zu beobachten). Das subepidermale Gewebe ist also nicht als Phellogen tätig gewesen, sondern als ein »Pseudophellogen», das anstatt der Korkzellen nur eine einzige kutinisierte Schicht produziert hat. Da die Schutzfunktion dieser neuen Zellschicht mit stark kutinisierter Aussenwand der der früheren Epidermis gleichwertig sein mag, kann hier fast von einer echten Regeneration gesprochen werden.

74. *Sedum spectabile* Boreau. — *Phytomyza sedicola* Hering (verosimiliter), cf. Küster (1903).

75. *Sonchus arvensis* L. X. — (*Phytomyza atricornis* Mg.) Gang in Palisaden- oder Schwammparenchym, bis an die Epidermis reichend.

76. *Stellaria holostea* L. III. — (*Scaptomyzella incana* Mg.) Mine im Schwammparenchym, teilweise auf die Palisaden übergreifend, mit Parenchymresten an der Epidermis. Hier treten natürliche Spalten im Gewebe auf. Kallus fehlt.

77. *Taraxacum officinale* Web. V. — (*Melanagromyza pulicaria* Mg.) Der Minenverlauf ist hier ähnlich wie bei Nr. 27. Es finden sich mehrere Gänge im Grundgewebe des Medianus, wohin die Larve immer wieder zurückkehrt. Weder hier noch in den seitlichen Abzweigungen wird Kallus gebildet.

78. *Thea assamensis* Mast. et *sinensis* L., — *Melanagromyza theae* Green. Die Larve frisst nur im Innern der Epidermiszellen der Oberseite, deren Aussenwand + Kutikula erhalten bleibt und sich auf die Palisaden legt; bei den darunterliegenden Palisaden erfolgen dann Teilungen durch

1—2 Querwände. Wo durch das Puparium-Lager die Epidermis-Aussenwand abgehoben ist, bildet das Palisadenparenchym mehrere Schichten von Kallus, auf denen das Pupar ruht. cf. DE MEIJERE (1934).

79. *Tilia platyphyllos* SCOP. VII. — (*Bucculatrix thoracella* THNBG.). Das gesamte Mesophyll zwischen den Epidermen ist verzehrt, nirgends Kallusbildung, auch nicht in der Nähe der Gefässbündel.

80. *Triglochin maritimum* L. IX. — (*Liriomyza triglochinae* HEND.) Gang nur in dem aerenchymatösen Zentrum des Blattes, ohne Verletzung der Palisaden, ohne Kallusbildung.

81. *Tropaeolum majus* L. — (*Scaptomyzella flava* MG.). Platzminen im Palisaden-Parenchym, stellenweise bis zur unteren Epidermis reichend. Auch obere Epidermzellen werden (mit Ausnahme ihrer Aussenwand) gefressen. Meistens ist eine Digressionszone gegen das Schwammparenchym ausgeprägt. Kallus fehlt auch dort, wo Leitbündel angeschnitten wurden.

82. *Tussilago farfara* L. X. — (*Acidia cognata* WIED.) Das 1. Stadium des Ganges verläuft in den Palisaden.

83. *Ulmus scabra* MILL. X. — (*Nepticula ulmivora* FOL.) Gang zuerst in den Palisadenschichten, später wird das gesamte Parenchym gefressen, Reste finden sich an der unteren Epidermis. Epidermis zuweilen angebissen, nekrotisch, besonders dort, wo Exkremente ihr ankleben. Auch am Leitbündel keine Kallusbildung.

84. *Vaccinium vitis-idaea* L. III. — *Nepticula weaveri* STT. Gang in den oberen 2 Palisadenschichten, dann mehr im Schwammparenchym. Das Minenlumen ist grösstenteils mit Kotballen gefüllt. Solange die Mine nur im Palisadenparenchym verläuft, wachsen aus dem Schwammparenchym einige Kalluszellen hinein, die nicht grösser als gewöhnliche Schwammparenchym-Zellen sind, die auch Lücken in der häufigen Digressionszone durchwachsen, Kallus-Bildung sonst sehr spärlich.

85. *Valeriana officinalis* L. VII. — *Liriomyza strigata* MG. Über den Leitbündeln des Medianus ist das Grundgewebe verzehrt, in den seitlichen Abzweigungen der Mine (vergl. Nr. 27) das Schwammparenchym. Kallus findet sich vereinzelt, die Zellen sind gross, mit deutlichen »Pektinwärzchen».

86. *Viscum album* L. III. — (*Argyroploce woodiana* BARR.) Der Jugendgang in den 4—5 oberen Parenchymschichten, sein Innenraum ist vollständig ausgesponnen, weshalb sich Kallus nie entwickeln kann. Die Epidermis über dem Minenraum ist immer abgestorben.

B. Allgemeiner Teil.

(Die in ( ) gestellten Ziffern bezeichnen die Nummer des Befundes im 1. Teil.)

I. Die Art der Veränderungen.

Es fällt bei der Untersuchung der Wundgewebe in Minengängen auf, dass die Totipotenz der Pflanzenzelle hier nur sehr wenig in Erscheinung tritt. Dort, wo Neubildungen sich zeigen, sind sie von einer relativen Einförmigkeit. Es sind vier Gruppen von Gewebeveränderungen zu beobachten, von denen die zuerst zu besprechende vorherrschend ist.

1. Kallus-Bildung. Aus Kalluszellen bestehen die am weitesten verbreiteten Wundgewebe überhaupt, dementsprechend werden sie in den Minen sehr häufig angetroffen. Sie sind hier wie auch sonst dünnhäutig, plasma- und chlorophyllverarmt. Ihr Gegenstück, der Wundkork, wird, wie schon Gertz (1918) für die Minen und Küster (1925) für die Gallen feststellte, nicht angetroffen. Auch in Minenhohlräumen mit relativ niedriger Luftfeuchtigkeit tritt der in trockener Luft sich leichter entwickelnde Kork nicht auf. Die Grösse der einzelnen Kalluszellen ist sehr verschieden und wird oft durch das Lumen der Mine bedingt oder geändert. Der Nukleus wird fast nie verändert angetroffen. Nur sehr selten ist die Chlorophyll-Lagerung relativ ebenso dicht wie in einer normalen Zelle, von der aus Kallus gebildet wurde (23, 27). Sonst lassen Blässe und Zartwandigkeit sie auf den ersten Blick von ihrer Umgebung unterscheiden. Sie sind sehr ähnlich Thyllen oder thylloiden Geweben, wie sie manchmal in andere Hohlräume der Pflanze hineinwachsen. Wie sie aus Parenchym hervorgehen, tragen sie auch meistens parenchymatösen Charakter; seltener nähern sie sich, namentlich in Zellschläuchen, schon mehr einem prosenchymatischen Habitus (4, 39; Text-Abb. 3, Taf. I: 9). Manchmal zeigen sich bei ihnen zipfelige Vorsprünge (53; Text-Abb. 11). Ursprünglich ist wohl jede Kalluszelle etwa kugelig; bei stärkerem Druck flacht sie sich ab und wird prismatisch. Eine besonders häufige Erscheinung sind Erhebungen auf ihrer Zellwand, die als »Pektinwärzchen» gedeutet worden sind; sie finden sich in den verschiedensten Grössen auf den Zellhäuten, die frei in das Lumen der Mine hineinragen, nicht aber dort, wo Kalluszellen in einem geschlossenen Verbande auftreten. Ob es sich wirklich um Pektinausscheidungen handelt,

kann vielleicht bezweifelt werden, da in manchen Fällen diese Gebilde als fast abgelöste kleine Kügelchen erscheinen (10; Text Abb. 5), so dass man sie fast als Mikroorganismen ansprechen möchte. Es würde verständlich sein, wenn sich solche auf den besonders zarten Zellhäuten des Kallus ansiedeln würden; das Innere des Minenganges ist ja durchaus nicht so steril, wie noch Portier (1918) angenommen hatte. Bemerkenswert ist ihre starke Tingierbarkeit durch Safranin. Selten beobachtet man solche »Pektinwärzchen» auch auf normalen Zellen, wenn sie an den Hohlraum angrenzen. Überwiegend entwickelt sich der Kallus aus dem Parenchym des Blattmesophylls, besonders aus dem Schwammparenchym, oder aus dem Grundgewebe der Blattrippen, doch können Kalluszellen auch aus anderen Elementen des Blattes sich entwickeln. Eine besondere Stellung nehmen die Bildungen ein, die man in den (selten) im Xylem verlaufenden Minen findet (37; Text-Abb. 9, 10). Sie sind offenbar aus Holzparenchymzellen hervorgegangen und scheinen von anderer Beschaffenheit zu sein als die aus dem Mesophyll gebildeten. Darauf weist schon ihre ausgeprägte Tüpfelung hin, und ihre intensive Tingierbarkeit lässt vermuten, dass die Zellwände wenn auch in geringem Grade verholzt sind. Man könnte hier schon von einer trachealen Umbildung der Kalluszellen sprechen, wie sie Küster (1925) als seltene Erscheinung bei Orchideen konstatiert. Im übrigen mangelt es dem Kallus durchaus an Differenzierungsvermögen; ein solches kann manchmal vorgetäuscht werden, wenn durch den Kallusdruck Gewebe-Elemente anderer Art von ihrem normalen Orte abgedrängt und ins Innere des Kallus verlagert werden, wie es bei Sklerenchymfasern (57; Taf. I: 6) und trachealen Elementen (4; Text-Abb. 1) geschildert wurde, die man nicht als umdifferenzierte Kalluszellen auffassen darf. Die namentlich im Grundgewebe der Blattrippen so häufigen Kristalle von Kalziumoxalat fehlen im Kallus immer (auch in gallentragenden Blättern wurde Kristallverarmung beobachtet). Die Kalluszellen treten zuerst isoliert im Minengange auf und bleiben es, wenn in ihm ungünstige (wohl Feuchtigkeits-) Verhältnisse herrschen. Unter günstigeren Bedingungen aber vermehren sie sich sehr stark und liegen dann, dicht gedrängt, ungeordnet im Hohlraum. In anderen Fällen dagegen erfolgt eine gerichtete Vermehrung; sie erscheinen dann in Schläuchen oder Fäden aneinander gereiht; das geschieht namentlich dann, wenn sie aus Markstrahl-Zellen entstanden sind, deren Richtung sie dann

auch öfter beibehalten. Bemerkenswert ist dabei, dass sie offenbar keine Polarität besitzen, sondern sowohl zentrifugal wie auch zentripetal wachsen können.

2. Vergrösserung und übermässige Vermehrung normaler Zellen. Gegenüber dem häufigen Vorkommen von Kallus treten die Fälle zurück, bei denen unter dem Einfluss der Insektenminen noch Dauergewebe Veränderungen erfahren. Solche selten beobachteten Erscheinungen lassen sich besonders dort feststellen, wo auch im äusseren Habitus schon ein Übergang von der Mine zur Galle zu erkennen ist. Eine Vergrösserung der Grundgewebe-Zellen wurde im Medianus beobachtet (25), wobei dieser und die umgebenden Partien auch äusserlich schon als verdickt erschienen. Parallel dieser Zellvergrösserung (die sich nur unwesentlich auf die Nuklei erstreckte) ging eine Chlorophyllverarmung des assimilierenden subepidermalen Parenchyms der Rippen. Bemerkenswert ist dabei, dass trotz der mehrfachen Frassgänge im so vergrösserten Parenchym sich nirgends Kallusbildung in diesen Hohlräumen zeigte. Es will scheinen, als ob sich diese beiden Modi der Gewebe-Veränderung ausschliessen; in anderen Fällen dagegen kombinieren sich beide Vorgänge; in Minengängen im Petiolus, der nach aussen verdickt erschien, wurde ebenfalls Kallus gefunden, während ihre Umgebung eine unbeträchtliche Vergrösserung der Zellen des Grundgewebes aufwies (57—59); die Petiolus-Verdickung war aber zum grösseren Teile auf Druck des üppig entwickelten Kallus zustande gekommen, der sich namentlich dann bildete, wenn das Fibrovasalbündel, wenigstens sein Sklerenchymring, verletzt worden war. Bei gewissen an Compositen vorkommenden Pustelminen der Gattung *Cystiphora* sind die an den Hohlraum grenzenden Zellen schwach vergrössert und werden anscheinend laufend von der Larve abgeweidet (34). Hier kann man mit gleichem Rechte von einer Galle wie von einer Mine sprechen. Sehr häufig wird eine Emporwölbung der Epidermis als Folge des Druckes von übermässig üppig erzeugtem Kallus beobachtet. Es mag sein, dass in vielen der beobachteten Fälle die natürliche Elastizität der Epidermis für eine Streckung zur Erzielung dieses Effektes ausreicht. In gewissen Fällen wird jedoch eine nochmalige Teilung von Epidermiszellen erfolgen, eine Reaktion auf den vom Kallusdruck ausgehenden Reiz (10; Text-Abb. 4). Auch hier kann aber eine Übersteigerung der Reizreaktion eintreten, indem die Vermehrung der Epidermis-

zellen nicht mit der Verminderung des Parenchyms durch die Frasstätigkeit der Larve Schritt hält. Die Folge einer solchen Gleichgewichtsverschiebung ist dann eine Einfaltung der Epidermis (25; Text-Abb. 7), bei Minen in der Blattspreite häufig eine starke Verkrümmung und Verbiegung des Blattes (10, 23).

3. Gewebe-Restitution. Nur selten kann man beobachten, dass das Wundgewebe morphologisch und funktionell einen hinreichenden Ersatz für das von der Larve verzehrte darstellt. Nur bei dem geschilderten Fall an *Salix* (73) kann wohl von einer eigentlichen Restitution gesprochen werden, indem eine vom subepidermalen Parenchym gebildete Zellschicht, deren Aussenwand in analoger Weise kutinisiert wird wie bei der echten Epidermis, das Aussehen und die abschliessende Funktion einer echten Epidermis anstelle der durch die Larve zerstörten annimmt.

4. Nekrosen und Digressions-Zonen. Ein örtlich begrenztes Absterben von Zellpartien im minierten Blatt kann an den verschiedensten Geweben beobachtet werden. Nekrosen sind namentlich häufig an der Epidermis über dem Minenraum. Sie finden sich besonders dann, wenn der Minengang bis an die Blatthaut heranreicht, während sie oft ausbleiben, wenn an ihr noch Parenchymreste, und seien es auch nur kleine Bruchstücke von Zellen, hängenbleiben. Sind die Epidermiszellen selbst verletzt, so sterben sie immer ab, eine Wundheilung ist bei ihnen nicht möglich. Die Auskleidung der Mine mit Gespinst (wie bei vielen Raupen) verhindert die Epidermnekrosen nicht. Eine besondere Rolle spielen wohl die nekrotischen Parenchym-Zellen an den Wänden so vieler Minengänge (31, 37), die einen ± vollständigen Abschluss der Mine gegen die gesunden Gewebe bewirken. Sie sind immer bräunlich verfärbt, geben aber keine Korkreaktionen, so dass eine Verkorkung nicht vorliegt. Offenbar sind sie mit gerbstoffartigen Substanzen angereichert, und diese bewirken, dass eine Infektion der intakt gebliebenen Zellen und Gewebe nicht erfolgen kann. In vielen Fällen sind sie auch noch mit Substanzen imprägniert, die aus den Larven-Exkrementen stammen. Die Bildung solcher Digressions-Zonen ist besonders wichtig für das Weiterleben der durch die Miniertätigkeit beschädigten Gewebe, wohl überhaupt dafür, dass Frassbeschädigungen an der Pflanze ohne weiterreichende Folgen bleiben. Die Gerbstoffeinlagerungen in die abgestorbenen Zellen oder deren Bruchstücke an den Grenzen von Frassbeschädigungen

machen diese Digressions-Zonen antiseptisch und verhüten die spätere Erkrankung der benachbarten gesunden Gewebe. Man beobachtet diese Erscheinungen auch häufig an Epidermen, an die der Larvenkot herangedrückt worden war. Eine ähnliche Digressionszone wurde auch bei einer im Xylem verlaufenden Mine innerhalb des Kallus beobachtet (37), ohne dass dabei erkennbar war, wie sich diese auch bei Tinktion hervortretende Zone von den übrigen Zellwänden unterschied. Die Kalluszellen im Minenhohlraum sind gegen schädliche Einflüsse von Bestandteilen des Larvenkotes immun, wahrscheinlich wegen ihres besonders hohen Turgors. Oft kann man beobachten, dass durch Kallus eine Art von Abkapselung der Exkremente im Minengange erfolgt. Solche Digressionszonen mögen öfter vorhanden sein, als sie in Erscheinung treten. Wenig sichtbare intrazelluläre Veränderungen mögen ihre Bildung bewirken. Nicht immer sind diese Digressionszonen ganz lückenlos, und es kann vorkommen, dass diese Lücken von Kallus durchbrochen werden (84).

II. Die Orte der Veränderungen.

Umbildungen können sich in allen Geweben des minierten Blattes vollziehen, nicht überall aber mit der gleichen Häufigkeit. Es scheint, als ob ein höherer Spezialisations-Zustand die Möglichkeiten der Veränderung herabsetzt, und wir dürfen wohl die Elemente, aus denen sich Kallus besonders häufig entwickelt, als die weniger differenzierten bezeichnen.

1. Das Mesophyll. Der Grossteil der Minengänge verläuft im Blattparenchym, dementsprechend sind in den meisten Fällen hier auch Umbildungsvorgänge beobachtet worden.

Das Schwammparenchym ist weitaus am häufigsten der Produzent von Kallus. Vielleicht ist bei ihm schon eine Disposition dafür vorhanden, da es in seinen Lücken Luft führt, und auch anderwärts ist Kallusbildung bei Luftzutritt beobachtet worden. Das von ihm gebildete Kallusgewebe wächst in Minenhohlräume hinein, die sowohl in ihm selbst, wie auch im Palisadenparenchym gefressen wurden. Gewöhnlich beobachtet man dabei die typischen grossen, rundlichen Zellen. Neu gebildete Zellen können aber klein bleiben und prismatische Gestalt annehmen, wenn der Druck der schon gebildeten Kallusmassen ihre Streckung verhindert. Diese quantitative Hypoplasie ist am Kallus in Minengängen besonders

deutlich zu beobachten. Fast immer ist übrigens die Anzahl der Kalluszeilen in der Mine sehr viel grösser als die der ursprünglich diesen Raum einnehmenden Schwammparenchymzellen.

Das Palisaden-Parenchym kommt viel seltener als Produzent von Kallus in Frage. Wird hier eine Bildung beobachtet, so sind die Zellen klein und rundlich (10). Öfter wird in oberseitigen Minen das Vorhandensein von Kallus diesem Gewebe fälschlich zugeschrieben, wenn das mikroskopische Bild falsch gedeutet wird. Sein Ursprung zeigt sich, wenn man dem Zellzusammenhang nachgeht, doch meistens im Schwammparenchym. Manchmal ist in den Palisaden eine Chlorophyllverarmung als Ausdruck einer qualitativen Hypoplasie festzustellen, namentlich dann, wenn bei interparenchymalen Minen die untere Schicht der Palisaden verzehrt worden ist (21). Die verschiedene Häufigkeit der Kallusbildung in den beiden Blattparenchymen zeigt deutlich, wie verschieden verschiedene Gewebe der Pflanze auf den gleichen Reiz reagieren. In gewissen, seltener zu beobachtenden Fällen wandeln sich Palisadenzellen in Form und Grösse noch um (32; Text-Abb. 8); so kann sich auch die untere Palisadenschicht noch nachträglich in den Minenraum hineinstrecken (10), eine selten zu beobachtende Möglichkeit der Hypertrophierung von Dauergewebe. Bemerkenswert ist auch die Beeinflussung des Palisadenparenchyms durch intraepidermale Vorgänge bei den epidermalen Minen, wie sie die nachträgliche Querteilung von Palisaden zeigt (78). Auch bei Anthocyananhäufungen in der Epidermis wird öfter ein Übergehen der Anthocyanbildungen auf die Palisaden beobachtet.

2. Die Epidermis. In einer relativ geringen Anzahl von Fällen verläuft die ganze Mine ausschliesslich im Innern von Epidermiszellen (3, 49, 60), und es wird in solchen Fällen auch nur selten (73) Kallusbildung in den Hohlräumen beobachtet, die ja erst nach Zerfall der Innenwand der Epidermiszellen erfolgen kann. Häufig beobachtet man eine wohl auf Zellvermehrung zurückzuführende Streckung der Epidermis, die im Zusammenhange mit ihrer Emporwölbung durch den Druck der unter ihr liegenden Neubildungen steht. Dass das so wirkende Trauma schliesslich eine »Überreizung« der Epiderm und eine Übersteigerung seiner Reaktion bewirken kann, die sich in einer Einfaltung ausprägt (25), war bereits erwähnt worden. In sehr vielen Fällen bleiben die Epidermiszellen unverändert über dem Minenraum, namentlich dann, wenn an ihnen

noch Parenchymreste hängen, seien es selbst nur Bruchstücke der Zellen. Dass die Epidermis selbst Kallus bilden kann, ist wohl ausgeschlossen; an ihr hängende isolierte Kalluszellen (4; Text-Abb. 2) sind wohl aus Parenchymresten entstanden. Sehr häufig findet man auch Anthocyane in den Epidermiszellen; das ist namentlich dann recht auffallend, wenn sie nicht mehr mit dem Parenchym in Verbindung stehen (61). Die Anthocyanbildung beschränkt sich oft nicht auf die Zellen über der Mine selbst, sondern wird auch in deren Umgebung angetroffen, auch nekrotische Minenwände können damit imprägniert sein (70). Es gibt Fälle, in denen die Anthocyane für die Larve lebenswichtig erscheinen; *Vidalia cornuta* Sc. legt konstant im Blatt von *Senecio nemorensis* L. zuerst ± quer durch das Blatt eine Gangmine an, die die obere Hälfte des Blattes»ringelt», die sich unter dem Einfluss der Assimilatstauung intensiv rotviolett verfärbt, und nur in diesem verfärbten Teile macht die Larve den grössten Teil ihrer Entwicklung durch. Ähnliches beobachtet man an *Succisa* (*Phytomyza succisae* Hering) und anderen Arten. Eine abgelöste Epidermis kann sich in gewissen Fällen (Text-Abb. 4) fest mit Gruppen von Kalluszellen verbinden, die dann durch ausreichende Wasserzufuhr sie vor der über dem Hohlraum leicht möglichen Vertrocknung schützen. Häufiger allerdings erfolgt Absterben der abgehobenen Epidermis, namentlich dann, wenn das Innere der Mine mit Gespinst ausgekleidet ist, das den ungehinderten Zutritt der Luftfeuchtigkeit, die sonst im Minengange recht hoch ist, verhindert, oder aber durch die chemische Wirkung von Stoffen aus der Kotablagerung der Larve, die vielfach an die Epidermis erfolgt. Bei epidermalen Minen geht die Epidermis stets zugrunde; wie in solchen Fällen eine Restitution der verlorengegangenen Gewebe durch Kutinisierung von Parenchymzellen bewirkt werden kann, ist ausführlich dargestellt worden (73). Eine solche Heterotypie einer pflanzlichen Bildung ist besonders bemerkenswert; sie findet ihr Analogon in den bekannten Fällen von Kutinisierung von Kalluszellen-Wänden beim Einwuchern in Atemhöhlen u. a. Nur ist es hier nicht Kallusgewebe, bei dem sich eine solche Strukturveränderung vollzieht, sondern ± parenchymales Gewebe, wenn auch solches von meristematischem Charakter.

3. Die Fibrovasalbündel. Die Wirkung des Minenganges auf die Leitbündel kann namentlich bei den Minen beobachtet werden, die im Petiolus oder Medianus des Blattes verlaufen. Kleinere Bündel

im Mesophyll werden oft teilweise mit verzehrt, wenn auch allgemein zu beobachten ist, dass die Larve sie zu vermeiden sucht. Sogar Arten, die vorwiegend im Medianus oder Petiolus leben, gehen ihnen aus dem Wege (25, 77). Allgemein ist aber zu beobachten, dass in Minen, die in der Nähe von Leitbündeln verlaufen, die Kallusproduktion besonders üppig ist. Schon früher wurde gleiches auch bei andersartigen Verwundungen beobachtet. Je mehr das Bündel durch den Larvenfrass verletzt wurde, umso ausgesprochener steigert sich die Kallus-Produktion im Minengange. Vielfach genügt schon eine Verletzung des mechanischen Ringes, um das in Erscheinung treten zu lassen. In dem einen beobachteten Falle von Zellenvergrösserung im Medianus (25) erfolgte aber auch bei Verletzung des Fibrovasalstranges keine Kallusbildung. Bei dem so seltenen Verlauf des Minenganges im Xylem (37) ist der darin gebildete Kallus offenbar anderer Natur als der aus dem Mesophyll stammende und zeichnet sich durch starke Tüpfelung und offenbar ausgeprägte Verholzung aus. Von besonderer Bedeutung für die Kallusbildung in oder nahe dem Leitbündel sind sichtlich die Markstrahlen, von denen in den meisten Fällen die Neubildung ausgeht (57). Sie wird begünstigt durch die Tatsache, dass bei ihnen nicht erst eine Parenchymatisierung prosenchymatischer Elemente zu erfolgen braucht.

III. Die Wirkung der Gewebeveränderungen.

Die im Minengange erfolgten Neubildungen haben weitergehende Bedeutung auch für Gewebe aus der Nachbarschaft der verletzten Stellen. Am sinnfälligsten sind die Folgen der Pressungs-Erscheinungen, die auf die Übersteigerung der Reizreaktionen zurückgehen. Dahin gehört die Emporwölbung oder sogar Einfaltung der lebend gebliebenen Epidermis, die zu starken Verkrümmungs- und Verbildungserscheinungen des Blattes führen kann (10, 23). Aber auch auf das Insekt ist diese Übersteigerung nicht ohne Einfluss. So wie der Druck des neugebildeten Kallus die Exkremente auf engstem Raum zusammenpresst, können Larven aus dem Hohlraum herausgepresst oder zusammengedrückt und vernichtet werden. Doch können solche vereinzelte Fälle nicht etwa als Abwehrreaktion der Pflanze gegenüber dem Schädiger gewertet werden, da nur ein kleiner Teil von diesem von einem solchen Schicksal betroffen wird. Das in der Umgebung der Mine gelegene Gewebe

erfährt öfters Umdifferenzierungen des Zellinhalts, dieser erscheint verdichtet und getrübt (4, 15) und färbt sich mit Methylviolett 5 B abweichend besonders intensiv. Eine solche Metaplasie der Zellinhalte, die vielleicht mit der durch Störung der Abwanderung zusammenhängenden Assimilatstauung zusammenhängt, stellte Küster (1925) auch bei Gallenbildungen fest. Selbst rein epidermale Minen können in den darunter liegenden Parenchymschichten gewebefremde Kutinisierung (73) oder überzählige Teilungen (78) bewirken.

IV. Ursachen und Bedingungen der Veränderungen.

Was im einzelnen im Innern der Mine vor sich geht, damit es zu den geschilderten Um- und Neubildungen kommt, kann mit Sicherheit nicht gesagt werden. Namentlich sind wir uns über die Ursachen der Kallusbildung im allgemeinen nicht im klaren. Wenn schon Bertrand (1884) seine »loi des surfaces libres» prägte, wonach an freien Oberflächen (wie sie auch die Larve künstlich im Minenraum schafft) Mestomteile oder Kambium gebildet werden, wird man dies vielleicht als die Grundlage, aber auch nur als eine der Bedingungen ansehen können, die gleichzeitig mit anderen wirksam ist. Für die Kallusbildung sind verschiedene Faktoren verantwortlich gemacht worden, deren Wirksamkeit auf unsere Fälle aber erst noch untersucht werden muss.

1. Mechanische Kräfte. Es ist angenommen worden, dass das Aufhören des Gegendruckes der benachbarten, herausgefressenen Zellen die Kallusbildung bewirkt. Der nachlassende Druck soll Zellen von Dauergeweben veranlassen, sich zu teilen und zu wachsen, nachdem Teilung und Wachstum bei ihnen bereits abgeschlossen waren. Dem steht scheinbar die Tatsache von übermässiger Kallus-Produktion entgegen, wie sie hier mehrfach geschildert wurde. Doch kann eine Übersteigerung der Reiz-Reaktion eine Fortsetzung dieser Tätigkeiten bewirken, nachdem der auslösende Reiz längst aufgehört hat. Jedenfalls sind auf mechanische Kräfte (Druck) die prismatische Umformung der ursprünglich kugeligen Kalluszellen und die Emporwölbungen der Epidermis zurückzuführen. Der Kallus im Minengange muss Zwangsformen annehmen, und nur bei besonders erhöhtem Turgor bleiben die Zellen in ihrer ursprünglichen Gestalt erhalten. Auf mechanische Kräfte ist auch die

Abdrängung von sklerenchymatischen und trachealen Elementen ins Innere des Kallus zurückzuführen.

2. Osmotische Kräfte. Änderungen im osmotischen Druck sind für das Zustandekommen der Neubildungen besonders wichtig. Durch die Schaffung des Minenhohlraumes wird die Flüssigkeitsabgabe der ihn umgebenden Zellen sistiert und damit ihr Turgor gesteigert. Turgorsteigerung ist aber dem Wachstum der Zelle förderlich. Damit ist auch zum Teil die Tatsache zu erklären, dass in der Nähe von Leitbündeln, wo ungestörte und reichliche Wasserzufuhr gewährleistet ist, Kallus sich meistens besonders üppig entwickelt.

3. Chemische Einflüsse. Es ist ganz sicher, dass von den Gewebetrümmern und Zellresten, die im Minenraum liegen, chemische Wirkungen im Zusammenhang mit Zersetzungserscheinungen an ihnen ausgehen. In erster Linie kommt wohl aber die Wirkung gewisser in den Larven-Exkrementen befindlicher Stoffe in Frage (9, 22, 35, 39, 52). Selbst in Minen, in denen aus anderen Gründen Kallus nicht gebildet wird, beobachtet man einige Zellen, die in Kotlücken hineingewachsen sind. Die so häufig zu beobachtende »Verkapselung» von Kotballen durch besonders reichlich gebildeten Kallus weist auf solche Zusammenhänge hin. Küster (1925) hat auch bei Gallen den Einfluss von Kotablagerungen und toten Zellen mit für das Vorkommen von Kallus verantwortlich gemacht. Klarer ist wohl die Bildung von Anthocyanen durch die Assimilatstauung gegeben; man sieht seit langem Zuckeranreicherung als eine wichtige Ursache von Anthocyan-Ausbildung an. Wieweit die Haberlandtschen »Wundhormone» an den Bildungen beteiligt sind, müssen künftige Untersuchungen lehren. Von grösster Wichtigkeit sind die an die Zellen der Minenwände herantretenden veränderten Medien: Luft und ihre Feuchtigkeits-Sättigung. Eine hohe relative Luftfeuchtigkeit, im Optimum 85—94 %, ist ja am günstigsten für jede Kallusbildung. So fördert der Feuchtigkeitsgehalt der vielen durch Zerbeissen geöffneten Zellen zusammen mit dem nach aussen bestehenden Abschluss der Mine das Kallus-Wachstum. Wenn ausserdem auch noch Leitbündel angeschnitten wurden, wird die Versorgung des Innenraumes der Mine noch mehr intensiviert, und das ist wohl das wesentlichste Moment für die Üppigkeit des Kallus im Minenraum, wenn dieser in der Nähe der Gefässbündel verläuft.

4. Eigentümlichkeiten der Pflanze. Nicht bei jeder Pflanzen-Spezies sind die Vorbedingungen für Neubildungen in Minen in der gleichen Weise gegeben. Im Minengang der gleichen Insektenart kann bei einer Wirtpflanze Kallus sehr üppig auftreten (10) und im nahe verwandten Wirt (2) fehlen. In manchen Familien, wie bei den Monocotyledonen, ist Kallus nicht oder nur äusserst spärlich zu finden. Überall bei Pflanzenarten, bei denen auch unter normalen Bedingungen schizogene Lücken im Parenchym häufig sind (44—46, 76), wurde kein Kallus gefunden. Das stellt man auch bei Arten fest, die aerenchymatöses Gewebe fressen (30), obgleich es sich dabei um Pflanzen handelt, die an Standorten mit höherer Luftfeuchtigkeit vorkommen.

Von gewisser Bedeutung, die allerdings nicht überbewertet werden darf, ist der Abschnitt der Vegetationsperiode, an dem der verletzende Eingriff in die Gewebe stattgefunden hat. Der aus der Gallenkunde bekannte Satz, dass Neubildungen und Umformungen erfolgen, wenn die Gewebe noch jung und zum Teil nicht voll entwickelt sind, gilt auch in manchen Fällen für die Minierer. Besonders auffällig kann dabei der Vergleich von zwei Generationen der gleichen Insektenart sein, deren 1. Larvengeneration überreiche, die Herbstgeneration aber fehlende oder nur spärliche Kallusentwicklung im Minenraum bewirkt (4). In anderen Fällen findet man aber auch reichlich gebildeten Kallus noch bei im Spätherbst erzeugten Minen (57—59, 68).

5. Eigentümlichkeiten der Insektenart. Wenn man die Frage nach der Wirksamkeit chemischer Einflüsse auf die geschilderten Neubildungen bejaht, wie es hier geschehen ist, wird man auch annehmen können, dass von manchen Insektenarten stärkere, von anderen schwächere Impulse zu Neubildungen ausgehen. Es gibt unter den minierenden Dipteren zwei ausgesprochen polyphage Arten, die ziemlich wahllos eine grosse Anzahl von Dicotyledonen-Familien befallen. Bei *Liriomyza strigata* Mg. (27, 41, 53, 85), die allerdings ihre Mine immer nahe den Blattrippen anlegt, ist Kallus fast stets anzutreffen, gleichgültig, um welche Pflanzenart es sich handelt. Er findet sich aber auch an Stellen des Blattes, die von stärkeren Leitbündeln entfernt liegen. Bei der anderen Art, *Phytomyza atricornis* Mg., wurde dagegen nie Kallus in den Minen gefunden (25, 75), selbst wenn diese (wie oft bei dieser Art!) neben den Rippen entlang liefen. Hier dürften wohl feine, schwer nach-

weisbare Unterschiede in den Exkretionen der Arten vorhanden sein, die dieses verschiedene Verhalten des Wirtes bewirken. Ebenso auffällig ist das regelmässig üppige Vorkommen von Kallus in den Minen der *Lyonetia clerkella* L. selbst in Minen an Pflanzen, bei denen *Nepticula*-Arten ganz ähnliche und schwer unterscheidbare Minen anlegen, in denen kein Kallus gebildet wird. Arten, die ihren Minengang mit Gespinst auskleiden, das die Luftfeuchtigkeit von den Wänden abschirmt, solche, die in grossen Platzminen leben, in denen das gesamte Mesophyll herausgefressen wird, oder andere, die die Epiderm in Falten legen, wie *Lithocolletis*, und so in beiden Fällen die Luftfeuchtigkeit im Minenraum stark verringern, zeigen keine Kallusentwicklung oder nur einzelne solcher Zellen in den Minenwinkeln. Die regelmässige Ausbildung der bekannten »grünen Inseln» im herbstlich verfärbten Blatt bei bestimmten Arten von Minierinsekten weist auf eine viel weitergehende Beeinflussung der Pflanzengewebe durch die Art des Insektes hin als es zunächst den Anschein haben möchte.

V. Bedeutung der Bildungen für die Pflanze.

In keinem Falle können die um- oder neugebildeten Zellen dem Stofftransport dienen, wie schon Schneider-Orelli (1909) experimentell nachgewiesen hat. Ganz sicher stehen sie aber im Dienste der Wasserversorgung des Blattes. Sie spielen ferner eine Rolle als Füll- wie als Kittgewebe und können so Teile des Blattes, die durch die Minen gefährdet sind, vor Vertrocknung und Zusammenfallen schützen. Doch darf ihre Bedeutung in dieser Hinsicht nicht überschätzt werden, da sie leichtem Verfall ausgesetzt sind (73). Ihre Zellinhalt-Verarmung zeigt, dass es sich bei ihnen schon um degenerierte Zellen handelt, die in ihrer Lebensdauer den Dauergeweben nicht an die Seite gestellt werden können.

In allen Fällen kann von einer vollständigen Gewebe- oder auch nur Zellrestitution nicht gesprochen werden. Es handelt sich bei den geschilderten Fällen ausnahmslos um Hypertrophien, während die bei der Gallenbildung häufig so bedeutsamen Hyperplasien niemals angetroffen wurden. Diese Bildungen verwischen aber die Verschiedenheiten zwischen Blattminen und Blattgallen noch stärker, und es lässt sich eine Entwicklung von der Galle zur Mine (34) wie auch von der Mine zur Galle (25) beobachten. Es weisen diese Neu- und Umbildungen, ganz gleich, an welchem Ge-

webe des Blattes die Schädigung bewirkt wurde, immer die gleiche Eintönigkeit in der Bildung auf. Die Mannigfaltigkeit der pflanzlichen Gewebe ist bei allen im Innern der Mine zu beobachtenden Veränderungen einer ausgesprochenen Vereinfachung gewichen.

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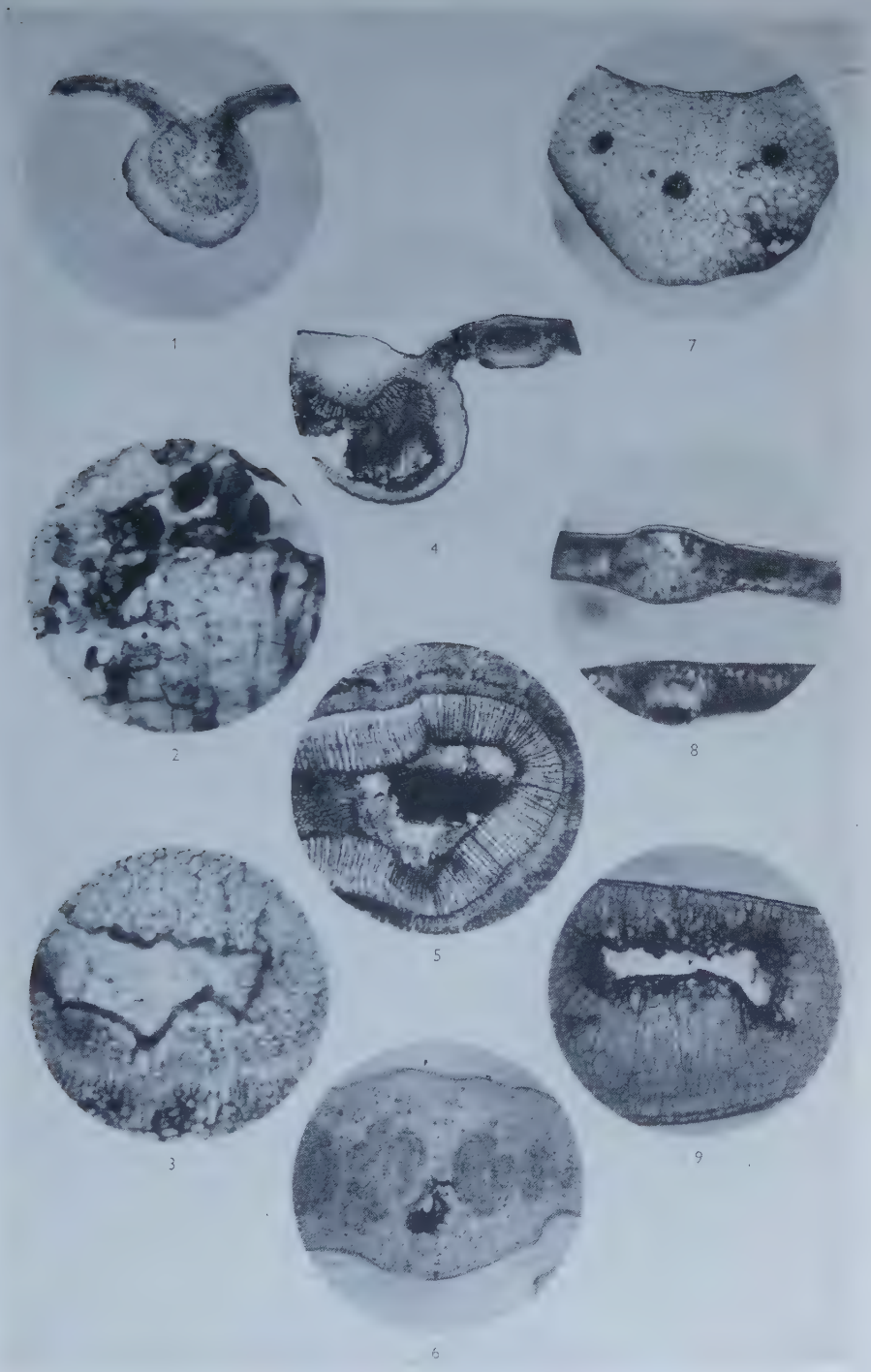
Tafel I.

Fig. 1. *Alnus glutinosa* (L.) Gärtn. Medianusquerschnitt mit Minengang von *Heliozela resplendella* Hw. im VII. Die Larve verzehrte den rechten Teil des Fibrovasalbündels einschliesslich des Sklerenchymringes, der ganze Hohlraum wurde mit dicht zusammengepresstem Kallus gefüllt, in dessen Zentrum die eng zusammengepressten Larven-Exkremente liegen. — Fig. 2. Die *gleiche Art*, Teil des Minenganges, stärker vergrössert. Kalluszellen noch nicht so dicht liegend, wachsen in parallelen Schläuchen in den Hohlraum hinein, Kotballen der Larve noch isoliert. — Fig. 3. *Ilex aquifolium* L. Querschnitt des Ganges von *Phytomyza ilicis* Curt. im Xylem des Medianus, mit Kallusfüllung, mit deutlicher Digressionszone gegen die erhaltenen Tracheen. — Fig. 4. *Betula pendula* Roth. Querschnitt des Medianus mit Minengang von *Heliozela betulae* Stt. Mine im Grundgewebe, greift auch Phloem und Xylem an, grösster Teil des Hohlraums wieder von Kallus gefüllt, der von den Markstrahlen des erhaltenen Leitbündelteiles entspringt und gegen das Grundgewebe durch eine deutliche Digressionszone getrennt ist. — Fig. 5. Die *gleiche Art* im 1. Stadium, im Innern der Sprossachse. Gang im zentralen Mark; nur stellenweise ist das Xylem verletzt, von diesen Stellen wuchert der Kallus in den Minenraum, die Exkremente zu einer einheitlichen Masse im Zentrum zusammenschiebend. — Fig. 6. *Populus italica* L. Querschnitt des Petiolus mit Gangmine von *Nepticula hannoverella* Glitz im 1. Stadium. Gang im Grundgewebe, Fibrovasalbündel nur mit geringen Spuren von Angriffen.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Reichliche Kallusmasse, die einen Teil des Sklerenchymringes dem Zentrum des Kallus zudrängt, wo schon die Exkremente der Larve zusammengedrängt sind. Petiolus einseitig schwach verdickt, Grundgewebe-Zellen schwach vergrössert. — Fig. 7. *Aster tripolium* L. Blattgrund-Querschnitt mit Mine von *Bucculatrix maritima* Stt. Das Grundgewebe hat nur schwach vergrösserte Kalluszellen gebildet, die Kalluszüge wachsen radiär zu dem Kotklumpen in den Minenraum hinein. Epiderm über der Mine nekrotisch. — Fig. 8. *Prunus virginiana* L. Teil des Blattquerschnitts mit Mine von *Lyonetia clerkella* L. Im Minenraum hat sich Kallus in solcher Üppigkeit gebildet, dass beide Epidermen nach aussen gewölbt worden sind. — Fig. 9. *Kleinia neriifolia* Hw. Querschnitt des Minenganges von *Liriomyza kleiniae* Hering. Zum Hohlraum sind von allen Seiten radiär Kallusschläuche gewachsen, deren Zellen teilweise prosenchymatisch erscheinen, und die die gebildete Digressionszone nach der Mitte zusammenschieben.

Phot. Kantak (Berlin).

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MACROPHYTE VEGETATION IN LAKES AND TEMPORARY POOLS OF THE ALVAR OF ÖLAND, SOUTH SWEDEN.

I. THE ALVAR AND ITS AMPHIBIOUS VEGETATION.

BY

HENNING HORN AF RANTZIEN.

The scope of the present study is a descriptive survey of the macrophyte vegetation (including vascular plants, bryophytes and charophytes) of the »lakes» and temporary pools of the limestone »Alvar» of southern Öland, Southeast Sweden.

The results are presented in two parts of which the present contains a general survey of the alvar and its »lakes» and temporary pools, a methodological and terminological chapter, and a description of the amphibious vegetation. The second part will be devoted mainly to the aquatic vegetation and to a general discussion of its correlation to the substrate.

With some exceptions, the nomenclature is in accordance with Hylander 1941 (vascular plants) and Jensen 1939 (mosses). Specific epithets have not been capitalized.

The writer is greatly obliged to Docent N. Albertson, Uppsala, Professor G. E. Du Rietz, Uppsala, Mr. C. Edelstam, Stockholm, Dr. phil. R. W. Kolbe, Stockholm, Mr. Sig. Olsen, Copenhagen, and Fil. kand. M. Witting, Uppsala, for valuable suggestions and positive criticism in various fields of the present investigation. Fil. kand. K. Thomasson, Uppsala, has kindly informed me about Esthonian alvar literature.

The Alvar — a Physiographic Survey.

The large island of Öland off the eastern coast of South Sweden is occupied in its southern half by a barren area, about 45×5—10 km, the southern alvar. As to its climate and geology, flora and fauna, vegetation and animal population, the alvar holds a distinct

position in North European nature geography. Mainly on account of the special qualities of this area, the local term »alvar» has been introduced into geographical and biological literature, though alvar areas are also found sparsely elsewhere in Northern Europe.

Albertson (1950) in agreement with Hesselman, Sterner, and others, defines alvar as a geographic term which is to be used for a limestone heath without any forest, where the rock (of Ordovician or Silurian origin) lies naked or is covered by a thin layer of soil — mainly products from the weathering rock.

The Öland alvar is the largest area without forest in South Sweden, and one of the largest alvars too; the vegetation has been described by Hemmendorff (1897) — the first survey and a fine one for that time — Sterner (1925, 1926, 1938, 1948, 1950), Albertson (1950) — with much references to the literature — and others. Smaller areas of the same kind are to be found on northern Öland (Sterner 1926, 1938), on the island of Gotland (see esp. Hesselman 1908, Du Rietz 1925, Bengt Pettersson 1946 a and b, 1949), and in Västergötland in the inner of southwestern Sweden (monographed by Albertson 1946). The largest alvars known are situated in Esthonia (Kupffer 1925, Lippmaa 1935, Thomson 1924, Vilberg 1926, 1927, 1929). Small fragments of alvar nature are present in Central Europe too (Du Rietz 1923, Kaiser 1926, Gams 1938, Meusel 1939). — Notes on alvar »lakes» and temporary alvar pools are to be found in Hemmendorff (1897), Sterner (1925, 1926, 1938, 1950) and Albertson (1950).

The bed-rock of the southern alvar is an Ordovician orthoceratitic limestone. Of its strata, the upper *Asaphus*-limestone is especially important as it forms the rock surface in large areas. It is a more or less reddish large-crystalline rock, not easily weathered, and of a thickness of about 2 m. The markedly stratified limestone is extremely flat. Rock fissures are rare, consequently drainage is very bad. On account of that, wide areas will be flooded also after a rather slight rainfall, and in spring parts of the alvar are shallow lakes. The surplus water flows slowly eastwards — the limestone bed slopes gently towards east — and the rest evaporates soon, except from deeper depressions. The quick and frequent changes between aquatic and terrestrial stages give rise to a rather peculiar kind of amphibious vegetation, where *Sedum* and *Cladonia* may occur together with *Agrostis* and *Scorpidium* on the same spot!

The alvar soil is mostly composed of a large amount of weathering products from the limestone, and of a small proportion of organic remains. On account of that, it is generally rich in lime particles (the upper layers of limestone contain c. 90 % Ca) but poor in humus and other nutritious elements, especially phosphoric acid. Generally, it has a basic soil reaction (pH about 8). Large areas of the alvar are furthermore covered by glacial melt and river deposits which are often poor in nutrition and have an acid soil reaction. They have been redeposited by the sea during the postglacial time.

A modern account of the geology of Öland has been given by Regnéll (1948, in Swedish). For details on the sedimentary rocks, see especially Moberg (1911), Hadding (1927—32), and Kaufmann (1931). Recent researches in the paleontology of Öland have been reported *e.g.* by Regnéll (1940, 1942). For a survey and details about the Late Quaternary changes in the sea-level of the western Baltic area, see Munthe (1904, 1940) and Thomasson (1927, 1935), and concerning the history of vegetation during postglacial time *e.g.* Lundqvist (1928). Sterner (1948) has given interesting accounts of the soil composition of the alvar and its importance for the vegetation.

The existence of alvar nature is connected with a cold temperate climate with a low annual rainfall. With respect to temperature, the climate of Öland is of the maritime type, while the conditions of precipitation are continental. Springs and autumns are thus late. Temperature observations from Öland are generally not directly applicable to the actual conditions on the alvar, as the meteorological stations are situated at the coast. Measurements are furthermore made 1.5 m above the soil surface. On account of the strong insolation, the physical character of the naked limestone rock, and the soil colour there is reason to believe that the temperature conditions are peculiar in the vegetation cover of the alvar. Falck (1913) measured air and alvar soil temperature in July 1912, and ascertained that there are great differences, the soil temperature having higher day values and a much greater temperature amplitude than that of the air. The island of Öland is a rather arid area as compared with other parts of Sweden. Average precipitation is about 430 mm pro year; minimum values for extremely dry years have been recorded down to 250 mm! The humidity values (*sensu* Hesselman 1932: precipitation in relation to average temperature)

are low and comparable to those of the West-Siberian steppes. There is a high amount of insolation — about 300 hours in June alone. Winds are frequent over the alvar with SSW winds predominating. In winter, bad drainage and frequent changes between frost and thaw cause peculiar physical phenomena in the thin soil, dislocations, corresponding to those observed in arctic conditions. — For details about the climate of Öland, see *e.g.* Wallén (1945), Ångström (1946), Bergsten (1948), and the papers of Sterner (esp. 1948).

The absence of spontaneous forest in the alvar is due to the thin layer of soil, the quick changes between flooding and complete drying up, and the dislocations of frozen earth in winter. Even human activity has influenced the development and accentuation of the alvar nature. Earlier, the alvar was a common of the villages of the Öland coast; especially the sheep grazing has been of great importance for the formation of present day vegetation. The grazing is now less intense, and probably will almost cease in some parts of the alvar. The result is likely to be an increase of the scrub-lands in areas where xeric meadows now prevail; especially the *Juniperus* shrubberies are likely to spread on moraine soil. Real forests will probably never develop here, except in the border zone of the alvar, where light and low, partly thorny, deciduous forests seem to be the climax vegetation.

Small parts of the alvar have a better drainage by means of deep rock fissures, partly filled up with good humus-soil. These areas differ in their vegetation from the rest of the alvar, and are termed »karst-alvar».

The mixture of different phytogeographic components, more or less foreign to the vegetation in other parts of South Sweden, is a rather distinctive feature of the flora of the alvar. For a discussion of these interesting matters, the reader is referred to the survey of Albertson (1950) and to literature cited by him, especially to the papers of Sterner (1926, 1938, 1948). It is sufficient to point out here that against an arctic-alpine component contrast an eastern continental steppe component and a southern, mediterranean lithic component. As a whole, however, the alvar flora makes a rather continental impression.

The continental resp. mediterranean components are characteristic of the alvar fauna too. Many examples are found *e.g.* among the insects (Wahlgren 1910, Mjöberg 1912, Jansson 1929, An-

DER 1948, 1949, etc.; esp. for Orthoptera ANDER 1930; Diptera RINGDAHL 1932; Lepidoptera WAHLGREN 1924, BENANDER 1930, 1932, etc.) but also among other invertebrates, esp. molluscs (HANSTRÖM 1948). GISLÉN (1947) has reported interesting results from an excursion to temporary alvar pools with finds *e.g.* of rare Phyllopoda. A survey of the alvar fauna and its immigration has been given by WAHLGREN (1915, 1917). Concerning the rich bird life, esp. of the alvar »lakes» and pools, see EDELSTAM (1948).

The alvar vegetation has a physiognomic resemblance to the true steppe vegetation of Eastern Europe as well as to the arctic and alpine mountain-heaths, but in fact differs from them both. It has been recently surveyed according to modern principles by ALBERTSON (1950). For all details the reader is referred to that informative paper. According to ALBERTSON the true alvar vegetation is composed of societies on more or less naked limestone rocks, grass and dwarfshrub heaths, xeric and mesic meadows. The »lake» and pool vegetation was not described in detail by ALBERTSON but only dealt with in short. It is the subject of the present paper and includes amphibious communities, namely meadows, heaths[1], marshes and swamps, and furthermore a number of aquatic societies.

Within the naked rock vegetation, ALBERTSON distinguishes a *Lecanora calcarea - Verrucaria nigrescens* association, a true terrestrial society with many xeric components, a *Collema cristatum - C. tunaeforme* association, characteristic of the annually submerged rock areas, and finally, a *Sedum album - Tortella tortuosa* association, which is a more advanced succession stage of the two latter lichen societies with many mosses, succulents and therophytes as significant components. — ALBERTSON divides the alvar heaths into three types too. The *Festuca ovina - F. rubra* v. *oelandica - Tortella tortuosa* association and the *Helianthemum oelandicum - Festuca ovina - Cetraria islandica* association are characteristic of the calcareous alvar soil. The latter is a terrestrial and xeric association, the former is found in areas annually submerged. The third type of heath, the *Sedum rupestre - Festuca ovina - Rhacomitrium canescens*

[1] The use of the term »amphibious heath» may cause some surprise. The local steppe communities discussed are peculiar transitional stages between heaths and marches, which are not appropriately to be included in any of them. With respect to the general physiognomy of the vegetation, they closely resemble some types of true heaths. A suitable term is difficult to find, however.

association, is characteristic of the moraine soil, ± rich in humus but poor in lime particles, and not or only occasionally submerged. — The xeric meadows (*Avena pratensis - Sesleria coerulea - Camptothecium lutescens* association) are found on comparatively thick layers of glacial deposits. The soil is never submerged. In some respect the xeric meadows are the most pronounced steppe communities of the alvar with a strong representation of interesting continental components. — The mesic meadows (*Sesleria coerulea - Molinia coerulea - Ctenidium molluscum* association) finally, are found on comparatively deep, annually flooded alvar soil. Where the soil conditions are especially favourable and grazing is slight — as *e.g.* in some parts of the easternmost marginal zone of the alvar — the latter association shows a deviating composition and physiognomy: dense *Potentilla fruticosa* shrubberies with *Cnidium*, *Serratula*, sometimes *Filipendula ulmaria*, etc.

The Lakes and Temporary Pools of the Alvar.

There are shallow depressions in the Ordovician limestone bed of the alvar which are temporarily or permanently filled with water. Evaporation is rapid, furthered by strong insolation and complete exposition to the winds. On account of that many depressions dry up in short time. The smaller alvar pools[1] (the local Swedish term is »vät» plur. »vätar») are annually water-filled in spring, but dry up in summer. After rains, they are often water-bearing in summer time too, but then the aquatic aspect is of short duration. The frequent changes in water level are endured only by a limited number of plants which form a peculiar kind of amphibious vegetation, not to be found outside the alvar areas proper. This type of amphibious vegetation is also met with on the shores of the alvar lakes[1] which, in their deeper parts, hold water even in summer except in years with exceptionally low precipitation. A true aquatic vegetation is generally to be found in their centre.

[1] There is an elaborate terminology in the limnological literature as to different categories of bodies of water (see *e.g.* Welch 1935). The writer is aware that the use of »lake» and »pool» as terms for alvar waters are not in agreement with the strict limnological concepts. Suitable names of these peculiar biotopes are not easy to find, however; besides, the term »alvar lake» has already been introduced into the literature (Sterner 1938, Albertson 1950: Germ. »Alvar See»).

With respect to the geology of the lakes and pools on the alvar, reference is made to the preceding chapter. The Ordovician limestone varies greatly as to its resistance to weathering. For the alvar lakes, having comparatively large tributary areas comprising different weathering types of limestone, this variation is probably not essential. It may be of importance to the small alvar pools, however. The contrast may be more essential between the Ordovician limestone bed with its calcareous weathering products, and the glacial melt resp. river deposits of moraine, sand, gravel etc., the latter being poor in lime and generally having an acid soil reaction. This contrast and its consequences for the terrestrial vegetation has been pointed out by Sterner and others.

In most cases, the topography of the basins and shores is rather simple. The larger basins are often characterized by a N–S length axis. They form shallow, even, bowl-shaped depressions in the limestone bed. Sudden and strong level differences are rare. Often one of the shores (esp. the eastern one) is formed by a somewhat steeper slope, sometimes overlayed by a moraine wall. The greatest depth — which does not generally exceed 1 m — is in the centre of the basin, but may also be found in the eastern part, near the steeper slope of the shore. When the basin is evenly bowl-shaped with its deepest part in the centre, the vegetation generally shows a distinct concentric zonation.

Most alvar lakes and alvar pools are seepage lakes: they have no marked or delimited tributaries and outlets. During rainy weather and in thaw, water trickles rather irregularly from the whole tributary area. When the passpoint of the basin has been reached, the water flows farther eastwards over the alvar.

The shores of all smaller pools are entirely minerogeneous. This type of shore prevails in the lakes too, though here organogeneous litoral deposits are met with to some extent. In some few lakes, shores of the latter type are more richly represented. The organogeneous shores sometimes consist of *Carex*-peat, formed in a more humid climate in Postglacial time. During present climatic conditions no formation of peat is likely to occur. As the scanty deposits are subjected to erosion by ice and waves, they are reduced year after year. — The minerogeneous shores are mostly naked limestone rocks, sometimes with a thin layer of weathering products (alvar soil); in some cases, however, with moraine or other glacial deposits, mentioned above, or with a layer of limnic chalk formed during high water.

Fig. 1. Shorebarricade in the southeastern part of Möckelmossen. Above the stones a narrow strip of *Carex panicea* meadow, to the right changing into a *Sesleria* meadow. Towards left, below the stones, a fragmentary *Agrostis stolonifera* heath. July 16, 1949. Photo: the writer.

Stone barricades formed by ice pressure have been observed at some larger alvar lakes (Möckelmossen and the alvar lake at Fröslunda) where moraine layers are found. Compared with the shore barricades found at many lakes of the Swedish mainland, those of the alvar lakes are quite small. For a detailed study of shore barricades and their origin in the upland of South Sweden, see especially THUNMARK (1931, pp. 11 ff.).

The water of the alvar lakes is characterized by a rather fluctuating hydrogen-ion concentration, a medium alkalinity, a generally high, though fluctuating Ca-content, a low content of chloride, and faint colour. These characteristics of the water depend upon the limestone bed and the low humus content of the alvar soils. No quantitative measurements of nitrates and phosphates have been carried out; as the weathering products of the limestone are poor in these compounds it is probable that the content of them in the water will prove to be low too. They may be locally increased by manuring by birds or grazing cattle.

In Tab. I, some few analyses of alvar water have been put together. The methods are described below. Particulars about the localities are to be

found in Part II of the present paper. All analyses of the water samples — kept in flasks of Jena glass — were carried out immediately or within 4 hours. — It may be added to the table that WITTING (1948, p. 133) found a Ca-content of 91.6 lmg in open water of the alvar lake Möckelmossen (measured spectrographically).

It is to be noted that the period July 16—26, 1949 during which all the samples were collected was unusually rainy. For that reason, the hydrogen-ion concentration, the total hardness, and the values of chloride actually registered are likely to be somewhat lower than those found during summers with more normal precipitation. The largest chloride content measured (36 lmg) is evidently due to pollution (manuring by grazing cattle).

The Hydrogen-ion Concentration was measured colorimetrically by standard solutions (hydrochloric acid, citrate, primary potassium phosphate, secondary sodium phosphate, borate and caustic-soda solution, see S. P. L. SØRENSEN 1909) and with the indicators generally used (brom phenol blue, brom cresol green, brom cresol purple, brom thymol blue, phenol red, and thymol blue). »pH act.» in the table indicates the actual hydrogen-ion concentration, measured directly in the water. In order to show the pH amplitude, the figures »pH min.» (= artificial minimum pH measured after blowing in pulmonary air) and »pH max.» (= artificial maximum pH, after boiling in Jena glass) have been given (see IVERSEN 1929).

The Alkalinity is an expression for that amount of acid which is to be added to the water to put down the hydrogen-ion concentration to 4.4. At this point, all bicarbonates have changed into CO_2. The alkalinity is expressed in mval/l. It has been measured titrimetrically by hydrochloric acid with phenolphtalein and methylorange as indicators. The contents of bicarbonates and carbonates (lmg HCO_3' and CO_3'') have been directly calculated from the alkalinity values. See DS [Dansk Standard], leaflet 213.

The Total Hardness has been determined titrimetrically by potassium palmitate (see DS 213). It is expressed in °DH (German Degrees), each degree corresponding to 10 lmg CaO. The method is not very exact but the values are sufficient for the present investigation.

The Chloride Content has been investigated in the ordinary way by titration with 0.0282 n silver nitrate with a solution of potassium chromate as indicator (DS 210) and is expressed in lmg.

The Colour of the Water has been measured according to HAZEN (1892) by a standard solution of potassium platinum chloride and cobalt chloride in hydrochloric acid. It is expressed in °Hazen (= lmg Pt).

Only few lakes in Sweden have shallow basins and plane surroundings to the same degree as the alvar lakes, where even a slight amount of rain will set large areas of rock and soil under water. The relatively large contact surface between water and bottom is supposed to cause a relatively large outflow of Ca-ions from soil to water. The alvar soil is probably the main contributor of Ca-ions. When the water evaporates, a process which is

Tab. I. Water-analyses from some alvar lakes and pools.

Locality	Date	pH			alka-linity	HCO_3' mg/l	CO_3'' mg/l	°DH	Cl mg/l	colour Pt mg/l
		min.	act.	max.						
Lake Möckelmossen:										
open water, surface sample, mats of *Chara aspera* in 0.5 m depth	$^{20}/_{7}$	6.1	6.5	8.7	1.0	61	0	7	17	21
lagoon at the eastern shore, filled up with *Chara aspera* and *Littorella*	$^{17}/_{7}$	6.5	7.1	8.2	2.4	143	0	$17\,^{1}/_{2}$	28	—
Alvar lake at Fröslunda:										
open water, surface sample, mats of *Chara aspera* in 0.4 m depth	$^{26}/_{7}$	6.6	7.4	8.7	1.5	91	0	$14\,^{1}/_{2}$	21	34
Alvar lake at Ebbelunda:										
open water, surface sample, single *Chara aspera* in 0.2 m depth	$^{26}/_{7}$	6.3	7.5	8.4	2.5	152	0	8	12	12
Polluted, permanent alvar pool, 500 m SW of southern end of Möckelmossen, surface sample in *Potamogeton natans* society, mats of *Chara vulgaris* in 0.1 m depth	$^{16}/_{7}$	6.1	6.5	8.6	1.1	85	0	8	36	16
Permanent pool in limestone quarry, 1 500 m SW of Ölands Skogsby, surface sample, mats of *Chara contraria* in 0.5 m depth	$^{17}/_{7}$	6.0	6.6	8.6	1.5	88	0	6	27	32

quick in summer on account of the high temperature, the exposition to winds, and the extensive water surface in proportion to the small water volume, the concentration of Ca will increase. Mainly by biological agents (Lundqvist 1940, p. 58), a great deal of the Ca dissolved is concreted into lime particles. The high Ca-content of the sediments is partly due to the latter process.

It has been mentioned above (cf. also the first chapter), that the weathering products of the limestone generally have a low humus and phosphate (probably also nitrate) content. For that reason the water in the alvar-lakes is likely to be poor in these compounds too. The small amounts of humus, phosphates and nitrates may be of decisive influence for the absence of a number of species occurring on eutrophic sediments. A relatively large amount of Ca and small content of other important elements may result in an »inharmonic water». Such a water, where the chemical composition is dominated by Ca-ions was considered by Naumann (1932, p. 112) to be characteristic of a certain type of lake, the alkalitrophic lake type. This concept has been subjected to criticism by other limnologists (*e.g.* Lohammar 1938, p. 242, Nygaard 1938, p. 605). The reason is that lower Ca values have been recorded in many lakes, regarded by Naumann as exponents for the alkalitrophic type, than in several »eutrophic» ones. It is possible, however, that not the absolute amount of Ca is the deciding factor, but the amount of Ca in proportion to other chemical elements in the water. — In this connection it is to be noted that Lundqvist (1925, p. 116) reports an increasing biological production by supply of humus to the water of lakes of Gotland, characterized by more or less oligotrophic lime sediments. The explanation may be a neutralization of the lime surplusage.

The sediment deposits, their composition and distribution is a matter of considerable importance for the study of aquatic vegetation. The calcareous sediments have been the object of an investigation by Lundqvist (1940). In that paper 23 different types of calcareous sediments are described on the basis of their microscopical structure. The present writer has not been able to carry out such studies to any great extent; nor have any chemical analyses been made.

The sediments of the alvar lakes and pools are strongly calcareous. Generally, lime particles constitute about half or more of a given sediment volume. With respect to the lime content, two different main types have been distinguished, lime gyttja and limnic chalk. Wet samples of these two sediment types are usually distinguished directly by their colour and consistence, the former being a greyish, greenish or yellowish, soft and plastic material, while the latter has a whitish colour and a hard structure. When dry, both sediment types are whitish, however.

The sediments have been classified in the field by means of a HCl-test. From a given small volume of the wet or water saturated sediment — generally 2 cc — the lime has been removed by addition of hydrochloric acid. As limnic chalk consists of lime particles to 70 % or more (Lundqvist op. c., p. 7), only a comparatively small rest of organic matter (detritus, algal remains etc.) and mineral particles is left after the lime has been dissolved. When the lime particles amount to 30—70 %, the sediment has been classified as lime gyttja. For practical purposes, the limit between limnic chalk and lime gyttja has been set at a lime content of 3/4 of the total sediment volume.

In the present classification the lime gyttja is rather heterogeneous. In the analyses no distinction has been made between organic material and inorganic material other than lime. Nor has any distinction been made between detritus and algal remains. A few samples of lime gyttja have been microscopically studied after removal of the lime. From them it can be noted that 1. the major part of the organic remains consists of fine-detritus; 2. the content of diatoms is fluctuating, but in general high; 3. the content of other algal remains is generally insignificant; 4. humus particles are absent or of no practical importance; 5. the content of mineral particles other than lime is comparatively high in marginal sediments, and low in the sediments of the central part of the basin.

Lundqvist (1940, pp. 58—60) has pointed out that, in his sediment material from the limestone lakes of Gotland, there is a tendency to a decrease as to lime content towards deeper water and towards the vicinity of certain types of vegetation (reed-swamps). The same is clearly to be seen in the present material.

Limnic chalk is characteristic of all kinds of temporary alvar pools, where it is often the only type of sediment. In the alvar lakes, it is found in the marginal parts, belonging to the amphibious zone, and is furthermore often met with in the upper aquatic zone on elevated bottom. It is supposed to form a bottom poor in nutrition. In the lower amphibious zone, one can often observe a correlation between the local distribution of limnic chalk and that of the *Agrostis stolonifera* heath. In the aquatic zone, mats of *Chara aspera* is the only type of vegetation found on this kind of sediment. Still more often, however, fields of limnic chalk in the aquatic zone are barren of any macroscopic vegetation.

Lime gyttja has a more restricted local distribution. It is mainly to be found in the central deep parts of the alvar lakes, elsewhere in depressions in the aquatic and lower amphibious zone. The lime gyttja is supposed to be more rich in nutrition than the limnic chalk. In the lower amphibious zone, there seems to be some correlation between the local distribution of this sediment and that of

Fig. 2. Möckelmossen, southeastern part. Illustration of the correlation between vegetation and sediment in the lower amphibious zone. To right and left thin layers of limnic chalk without macrophyte vegetation. In centre a depression with accumulation of sediment, covered by *Scirpus palustris* - *Littorella* marsh (*Littorella* sociation). July 16, 1949. Photo: the writer.

the *Scirpus palustris* - *Littorella* marsh. In the aquatic zone, helophyte and isoetid societies are almost exclusively found on lime gyttja.

Two other types of soil of importance for the amphibious vegetation are to be described in this connection. One is the peat. On the alvar, peat deposits are only found in the lake basins. Typically, they are confined to the deepest, central parts but may be found in connection with the shore line too; the latter is then generally more steep than usual. For some further notes, see p. 78. *Carex elata* swamps and amphibious reed-swamps have been recorded from peat deposits. — The »alvar soil» is a characteristic mixture of weathering products from the limestone and organic remains. It is a fine-grained brownish soil of a neutral or basic reaction. It constitutes the most important substrate for all amphibious *Carex panicea* meadows and for certain amphibious *Agrostis stolonifera* heaths.

There is an interesting correlation between the thickness of the substrate and the type of vegetation. On the one side there are the naked limestone rocks or those provided with a thin (about 0.5 cm

thick) layer of sediment or soil. In the aquatic vegetation zone, areas of this kind are covered with societies of micro-algae. In the amphibious zone they are devoid of any vegetation besides some few tufts of amphibious mosses. Sediment layers of 1—2 cm thickness are generally covered by *Chara aspera*; soil-layers of the same depth in the amphibious zone are characterized by *Agrostis stolonifera* heath. Aquatic isoetid societies, amphibious *Carex panicea* meadows, and *Scirpus palustris - Littorella* marshes seem to require a thickness of the substrate which is about 5—10 cm, while aquatic reed-swamps and nymphaëid societies must have a substrate depth not less than 20 cm.

A division of the lake bottom into three zones according to substrate conditions and ice erosion has been carried out by THUNMARK (1931). His division has a general applicability to Swedish lakes; the zones and the limits between them are of importance for the local distribution of a number of aquatic plants and plant societies. In the alvar »lakes», however, the three zones are indistinct. The reasons may be their small size, rapidly changing water level, and shallowness.

According to the above, the alvar lakes of Öland may be characterized as lakes with oligotrophic lime sediments. Lakes of this type are met with in other parts of Sweden, too, though they are uncommon. In certain features, however, especially the climatic conditions and the basin configuration the alvar lakes differ from lakes of other limestone areas, characterized by the same kind of bottom.

The arid climate, the shallow basins and the bad drainage of the alvar give the alvar lakes a similarity to the true steppe lakes, described from different dry regions of the world. The rich bird fauna and the plant-life with its peculiar topographical arrangement and its many strange components intensify this impression. As a characteristic limnological feature of the steppe lakes (and of lakes of other arid areas, deserts, semideserts, etc.) has been emphasized the lability of their milieu spectrum in the same year or in the very same season of the year. This lability contrasts to the more stable conditions in lakes of more humid areas. As factors influencing these rapid biotope changes to a major degree are reported: the great and rapid evaporation, the wind transport of large quantities of soil particles, the transgression of the lake water over large areas of surrounding soil, etc. (see *e.g.* DECKSBACH 1924, p. 279). The factors mentioned are of considerable importance for the alvar lakes, too.

The general impression of the vegetation is another than that produced by lakes of the Swedish mainland. The shores lie ex-

posed, open and flat; reed-swamps or quagmires of tall *Carex* species do not form the usual mosaic along the edge. The margins of the alvar lakes are covered with green lawns of low *Carex* species, or of grey heaths dominated by *Agrostis stolonifera*. In the heaths, the soil is bare between the light culms or is covered by blackish *Scorpidium* or dead, white *Chara aspera*. Near the shoreline, we meet light marshes of low *Scirpus palustris*, species of *Juncus*, and *Littorella*. Here too the greyish or greenish lime gyttja is covered with the dead *Chara* or patches of brown *Drepanocladus sendtneri* and black or purplish *Scorpidium scorpioides*. There are furthermore barren areas of naked limestone, sometimes covered with a thin layer of limnic chalk, shining intensily white in the sun. By the gusts of wind the shallow greyish water of the alvar lakes is raised in ragged waves over the naked limestone bottom, where in other Swedish lakes we find aquatic reedswamps and nymphaeid zones. Further outwards, somewhat deeper, there are aquatic meadows of greyish or greenish *Chara aspera*. In the deepest, central part of the lake, where the lime gyttja has been accumulated in heavy layers, and where sometimes a sharp darkbrown shelf, excavated by waves and ice, announces the presence of rest-layers of peat, we find patches of nymphaeid and helophyte societies surrounding a quaking island of *Carex elata* tussocks.

This description refers to the typical alvar lakes. There are also transitions, however, to the vegetation arrangement of the average Swedish lake, where various amphibious communities and, below the shoreline, reed-swamps, nymphaeid and elodeid or isoetid societies form the typical zonation in the sequence mentioned.

As an especially characteristic feature of the alvar lakes is to be noted the splitting of the amphibious vegetation into two parts, between which there is a belt of true aquatic vegetation. In the marginal parts of the amphibious vegetation *Carex panicea* meaows, *Agrostis stolonifera* heaths, and *Scirpus palustris - Littorella* marshes prevail, while the central parts are inhabited by *Carex elata* swamps and sometimes by amphibious reed-swamps. Aquatic reed-swamps and nymphaeid societies are of little importance.

The floristic composition of the lake vegetation will be dealt with in detail in a later chapter, and therefore only some general notes will be made here. Floristically, the alvar lakes are especially notable by a number of peculiar combinations of species. As such may be mentioned the presence of a number of exacting basibionts (*e.g. Sesleria coerulea*, *Carex*

hostiana, *Scorpidium scorpioides*, *Drepanocladus sendtneri*) together with components which are common to oligotrophic limestone soil areas and acid soil areas (*e.g. Littorella uniflora*, *Apium inundatum*, *Myriophyllum alterniflorum*) and components common to calcareous freshwater and brackish water (*Scirpus tabernaemontani*, *S. uniglumis*, *Potamogeton pectinatus*, *Chara aspera*, *Campylium polygamum*, etc.). A significant feature is the absence of a number of characteristic eutrophic lake plants (*Iris pseudacorus*, *Potamogeton lucens*, *Ranunculus lingua*, *Sium latifolium*, etc.). — Besides the groups of components mentioned above, characterized by different biotope requirements, strongly contrasting distributional categories are represented. As extreme examples may be mentioned the arctic-alpine *Scorpidium turgescens*, the southeastern steppe-component *Plantago tenuiflora*, and the southwestern *Apium inundatum*.

Vegetation Methods and Terms.

The phytosociological system used is based upon the floristic affinity of vegetation types. By means of indicator species, that is species which are present in one plant community and absent in another, the different vegetation types are delimited from each other. The different vegetation types of higher or lower rank can often be correlated with biotope factors. They are characterized by a limited geographical distribution, and thus they are — as well as taxonomical categories — to be considered as geographical elements. Within the vegetation types, delimited according to the above, changes are often observed in the dominance of certain species.

With some exceptions, vegetation is generally built up by several layers. In most alvar vegetation is to be found a field-layer (grasses, herbs) and a bottom-layer (mosses, lichens). Now, one can study the combination of the layers (the whole vegetation cover), or the investigation can be restricted to one layer only. The former method has generally been used in the present paper, except with respect to the aquatic vegetation, where the affinity between the different layers is especially loose. Here, each layer has been studied separately. The layers distinguished in aquatic vegetation are based upon the lifeform (*sensu* Du Rietz 1921) of their components, *viz.*, for the alvar lakes, helophyte, nymphaeid, elodeid, and isoetid layers.

When an investigation is focused on the study of a combination of layers, *i.e.* the entire vegetation, the association is the unit of lowest rank which can be distinguished by the presence or ab-

sence of indicator species. Within the association, sociations are those subordinate units which can be made out by means of the dominant species. In the study of a certain layer of the vegetation cover (*e.g.* mossvegetation or helophyte vegetation), union and society are the units corresponding to association and sociation. When studying the dominance of a certain species, it can sometimes be useful to refer to the plant community dominated by it by a certain term, in spite of changes of dominance in another layer. The term used is consociation. — Aspect indicates the temporary physiognomy of any plant community.

An example taken from the present paper may illustrate what has been said above. On the shores of the alvar lakes and in the alvar pools, an amphibious plant community of heath[1] character occurs rather commonly. It has been termed the *Agrostis stolonifera - Alopecurus geniculatus - Scorpidium turgescens* association or simply, the amphibious *Agrostis stolonifera* heath. Its distribution is to some degree correlated to soil factors and to frequency and duration of the inundations. This heath is built up of a field-layer with *Agrostis stolonifera* and other grasses and herbs and a bottom-layer with *Scorpidium turgescens* and other mosses. All patches of this heath have a certain common floristic composition, they show floristic affinity. They are distinguished from other associations by a number of indicator species. To take some examples, they differ from the amphibious *Carex panicea* meadow by the presence of *Plantago tenuiflora* a. o., and absence of *Parnassia palustris* a. o., and from the amphibious *Scirpus palustris - Littorella* marsh by the presence of *e.g. Leontodon autumnalis* and absence of *Scirpus palustris*, etc. Within the amphibious *Agrostis stolonifera* heath there are a number of sociations delimited by means of dominant species in the different layers: an *Agrostis stolonifera - Scorpidium turgescens* sociation, an *Agrostis stolonifera* sociation without any bottom-layer, an *Alopecurus geniculatus - Drepanocladus sendtneri* sociation, etc. All sociations with *Scorpidium turgescens* dominating in the bottom-layer can be referred to the *Scorpidium turgescens* consociation, irrespective of the *Agrostis* or *Alopecurus* dominance in the field-layer. In spring, when the heath is flooded, *Chara aspera* grows luxuriantly here, but dies as soon as the water has disappeared in early summer. In spring, we meet the aquatic *Agrostis-Chara* aspect, in summer the terrestrial *Agrostis* aspect.

A bryologist, interested in the moss vegetation only, is likely to distinguish this heath as a union (perhaps termed the *Scorpidium turgescens - Tortella rigens* union). A *Scorpidium turgescens* society, a *Drepanocladus sendtneri* society, etc. can be distinguished according to the dominant species.

The phytosociological methods and terms in the present paper are the same as those extensively used in Scandinavian plant ecology after 1935 (see the surveys of Du Rietz 1942, 1949). The system is a compromise

[1] See footnote p. 76.

between the former methodology of the Upsala School as summarized by Du Rietz (1921, 1930) and the methods generally applied in Central European plant ecology (see *e.g.* Braun-Blanquet 1928, Engl. ed. 1932). Thus the square-quadrat method and the study of dominance (*i.e.* the distinction of plant communities of low rank: sociations and societies) are in accordance with the former system. The qualitative delimitation of units of high rank (associations, etc.; unions, etc.) by indicator species corresponds to the methods used in Central Europe. — Many plant ecologists divide the indicator species into »index species» and »differential species». Most Swedish sociologists — in agreement with the usage in Central Europe — express the units of different rank by certain Latin suffixes (thus *e.g.* Molinietum alvarense of the *Sesleria-Molinia-Ctenidium* association of the alvar).

In the above survey and example, terms have been defined and commented upon only if used in the present paper.

The writer has chosen the association as the principal unit for the present investigation. The choice of the association is not based on any belief that this unit should be of a more »natural» character or of more fundamental importance than any other plant community of high rank. For the present survey of a local area, the association is convenient to handle; besides, the alvar associations are rather easy to delimit, though transitions occur. — Comparatively little weight has been laid upon the changes in dominance within the associations, as these changes are often accidental in the vegetation described.

Generally, a survey of vegetation is supplemented by tabellary accounts. For the aquatic one-layer societies dealt with, this is hardly necessary as the number of components is small. The amphibious two-layer sociations have been partly comprehensively illustrated in previous papers by Albertson and others. For that reason the writer has desisted from tables in the text. My material of analyses from the plant communities described have been accounted by summaries in connection with the description of the associations. These summaries form but a selection of the analysis material. Their scope is to exemplify the average composition of the association and the changes in dominance within it.

When the association has been delimited by a general list (see Tab. III) including all species observed within it, and the indicator species have been studied, the analyses of the sociations have been performed by the usual square-method used in Scandinavian plant ecology. Within each sociation studied at least 10 squares (with an individual area of 25 dm^2) have been analysed. In each square all species present have been noted together with an estimation of the relative surface covered by the species in the square (Hult-Sernander scale of covering, where degree 1 indicates that the species covers $< 1/16$ of the square analysed; $2 = 1/16$—$1/8$; $3 = 1/8$—$1/4$; $4 = 1/4$—$1/2$; $5 = > 1/2$).

The examples given in the following chapter are summaries of 10 square analyses. They consist of lists of all plants found in the squares together with two series of figures. The figures immediately after the plant names, ranging from 1 to 5, indicate the extreme values of covering in the 10 squares

Tab. II. Comparative survey of the shore zonation terminology.

<table>
<tr><th colspan="3">Present paper</th><th rowspan="2">Thunmark 1931</th><th rowspan="2">Du Rietz 1939, 1940</th><th rowspan="2">Du Dietz 1950 a</th></tr>
<tr><th>Principal hydrographic lines</th><th>Principal vegetation changes</th><th>Principal vegetation zones</th></tr>
<tr><td>Extreme catastroph line of high water</td><td>Certain terrestrial components sensitive to inundation are killed</td><td>Terrestrial zone</td><td>Supralitoral</td><td>Eugeobiontic zone</td><td>Epilitoral</td></tr>
<tr><td>Normal, annual high water line or limit for the effective inundation by waves and spray</td><td>Change from a terrestrial to a mainly amphibious vegetation</td><td rowspan="2">Amphibious zone</td><td rowspan="2">In exposed shore sections: Supralitoral & Eulitoral
In sheltered shore sections: Eulitoral</td><td rowspan="2">Geoamphibiontic zone</td><td rowspan="2">Geolitoral</td></tr>
<tr><td>Normal, annual low water line</td><td>Change from a mainly amphibious to an aquatic vegetation</td></tr>
<tr><td rowspan="2">Extreme catastroph line of low water</td><td rowspan="2">Certain aquatic components sensitive to drought are killed</td><td rowspan="2">Aquatic zone</td><td rowspan="2">Sublitoral and Elitoral</td><td>Hydroamphibiontic zone</td><td>Hydrolitoral</td></tr>
<tr><td>Euhydrobiontic zone</td><td>Sublitoral</td></tr>
</table>

according to the Hult-Sernander scale, while the figures within brackets, ranging from 10 to 100, indicate (in %) the number of squares, in which the plant was found. »*Sagina nodosa* 1—2 (70)» thus indicates that this species was found in 7 of the 10 squares analysed and that the degree of covering varies between $< 1/16$ and $1/8$ of the individual squares.

This method of presenting the material saves expense and space but it does of course not give the same detailed picture of the plant community as a table; nor is it possible to reconstruct the vegetation of the individual square.

The zonation terminology used is the same as in my paper of 1950. It is a preliminary and local classification, but corresponds closely to recent shore zonation terminologies used in the Swedish literature. It is based upon the vegetation alone, but can be correlated with hydrographic lines. See Tab. II, and for a detailed discussion of terms used up to 1940 the survey of Du Rietz (1940).

Some few general ecological terms are to be dealt with in this connection. The terms eutrophic and oligotrophic are often used in varying meanings. In the present paper, they have been used only for the characterization of soils and sediments, and refer to the contents of nutrition. — The occurrence of a plant or plant community on soil of different water content has been expressed by the descriptive and comparative terms hydric, mesic and xeric (see Cooper & Weese 1926, p. 390) extensively used in the American bio-ecological literature. These terms do not express the nature of relation between plant and water (a hydric plant is not necessarily a »hydrophilous» one), nor do they express any definite amount of water in the soil. It is also to be noted that a species is often hydric in one type of vegetation, mesic or xeric in another.

Survey of the Amphibious Vegetation.

It has been pointed out in the first two chapters that the alvar is subject to frequent floods at rather irregular intervals. Because of the plane topography, large areas are submerged. The aquatic stages are of short duration, due to the strong evaporation.

A description of the »amphibious vegetation» of the alvar should consequently comprise a number of rather different plant communities. Some of them would be strange elements in a description of lake and pool vegetation, *e.g. Festuca ovina* heaths with a number of succulents and therophytes. For that reason, the present survey of amphibious vegetation has been confined to typical shore-plant communities only.

The ecological conditions in the amphibious zone are to some degree uniform. On account of that, the differences and changes observed in the vegetation can be correlated with a few factors, *i.a.* humus content, water storing capacity and depth of soil, ice erosion, flooding, and drying up.

Parallel with the changes in the water factor, three main vegetation zones can be distinguished. Characteristic of the upper zone is a strong representation of terrestrial components (*Carex hostiana, Leontodon autumnalis, Ctenidium molluscum, Tortella tortuosa*, etc.) together with a number of amphibious plants (*Carex panicea, Caltha palustris, Scorpidium lycopodioides*, etc.). In the

middle zone, typical amphibious plants (*e.g.* those mentioned above) prevail. Some terrestrial components are found together with them (*e.g. Prunella vulgaris*). In the lower zone, finally, the terrestrial species disappear except some few, *e.g. Mentha arvensis* f. *oelandica*. Genuine amphibious plants such as *Carex oederi* prevail. Together with them some aquatic components (*Littorella uniflora, Scirpus palustris, Ranunculus trichophyllus* f. *succulentus*, etc.) are to be found, which are lacking in the upper zones.

The shores of the alvar lakes above the low-water line are characterized by some few types of macrophyte vegetation. When typically developed, they are distinct and easy to classify. Transitions occur, however. Most of the vegetation types mentioned below were distinguished by Albertson (1950).

Firstly, there are three associations which are characterized and composed of mainly terrestrial plants, able to endure short submersions. They are not described in detail in the present paper, as they cannot be considered as really characteristic of lake shores. Though found in the »amphibious zone», in the widest sense of that term, they are more appropriately to be dealt with in connection with the terrestrial vegetation. The three associations are the *Sesleria coerulea* meadow (*Sesleria coerulea - Molinia coerulea - Ctenidium molluscum* association), the *Festuca-Tortella* heath (*Festuca ovina - F. rubra* var. *oelandica - Tortella tortuosa* association), and the *Collema* crust on naked, at times submerged limestone rocks (*Collema cristatum - C. tunaeforme* association).

The other associations are typical lake shore communities, largely composed of amphibious plants which not only endure but even require regular floodings for some, not too short time. Hereto belong the *Agrostis stolonifera* heath (*Agrostis stolonifera - Alopecurus geniculatus - Scorpidium turgescens* association), the *Carex panicea* meadow (*Taraxacum limnanthes - Carex panicea - Scorpidium turgescens* association), the *Scirpus palustris - Littorella* marsh (*Scirpus palustris - Littorella uniflora - Scorpidium scorpioides* association), the *Carex elata* swamp (*Carex elata - C. appropinquata - Scorpidium scorpioides* association), and, finally, the amphibious reed-swamp (*Phragmites communis - Lastrea thelypteris - Scorpidium scorpioides* association), which, however, is only fragmentarily represented in the alvar lakes.

1. The amphibious Carex panicea meadows.

During the dry high-summer time, the alvar plant communities lose their green colour and turn reddish or grey like the rock upon which they are growing. But also in times of drought we notice patches and bands of a vivid green in the upper and middle amphibious zones of the alvar lakes. The green areas which strongly contrast with the surrounding heath and marsh vegetation cover a better soil, which is deeper and more rich in humus, than that of the heaths. This type of vegetation was preliminarily distinguished by ALBERTSON (1950, p. 315) as the *Taraxacum limnanthes - Carex panicea - Scorpidium turgescens* association. In the field-layer the most important dominants are *Carex flacca, C. fusca, C. hostiana, C. oederi, C. panicea, Molinia coerulea, Potentilla anserina,* and *P. reptans.* In the bottom-layer, *Scorpidium turgescens* is perhaps not quite so conspicuous in the amphibious *Carex panicea* meadows of the alvar lakes as it is in the vegetation of the small, temporary alvar pools. *Drepanocladus sendtneri,* and to some degree also *Scorpidium lycopodioides* and *Campylium polygamum,* seem to be the most prominent dominants. *Ctenidium molluscum* and *Campylium stellatum* are important in the mesic types. The *Carex panicea* meadows are often rich in species; in this respect they exceed all other associations dealt with in the present paper.

The mesic types of the *Carex panicea* meadow are generally dominated by *Carex hostiana* (sometimes *C. flacca*) and *Molinia* in the field-layer and by *Campylium stellatum* and *Ctenidium* in the bottom-layer. Very often, the uppermost part of the amphibious zone is developed as an association-complex with the more terrestrial *Sesleria-Molinia-Ctenidium* association on the hummocks and the amphibious *Taraxacum - Carex - Scorpidium turgescens* association in the depressions between them. The *Carex hostiana* and *Molinia* sociations show a rather varying species composition. Outside the alvar proper, they are often rich in exacting species. Medium rich or rather poor sociations are generally met with on the shores of the alvar lakes. It is possible that the variation in species number and qualitative composition has some connection with the duration and frequency of inundations. For the alvar vegetation of Västergötland, South-West Sweden, ALBERTSON (1946, p. 120) has distinguished two variants of the *C. hostiana* consociation, a »hydrophilous» one, poor in species, and a »hygrophilous» one, rich in species.

Lower down on the shore more hydric types of this association are met with. Where the soil layer is comparatively thick and rich in humus, the principal dominant species are: *Carex panicea* (sometimes also *C. fusca*), *Drepanocladus sendtneri*, *Scorpidium lycopodioides*, and *S. turgescens*. Where the soil layer is thinner and poor in humus, sociations are developed which show affinity to the amphibious heaths.

The limit between the mesic *Carex panicea* meadow and the hydric types of the *Sesleria coerulea* meadow (*Sesleria coerulea - Molinia coerulea - Ctenidium molluscum* association of Albertson 1950, p. 310) is sometimes obscure. Although many field-layer components of the hydric *Sesleria coerulea* meadows proceed into the *Carex panicea* meadow, there are a number of amphibious plants, which seldom or never are found in a meadow of the former type. As such differential species of the *Carex panicea* meadow against the *Sesleria* association may be mentioned: *Alopecurus geniculatus*, *Carex fusca*, *C. oederi*, *Equisetum palustre*, *Eriophorum latifolium*, *Juncus alpinus* ssp. *australis* and *J. articulatus*, *Scirpus planifolius and S. pauciflorus*, *Caltha palustris*, *Galium palustre* ssp. *eu-palustre*, *Inula britannica*, *Mentha aquatica*, *Pedicularis palustris*, *Polygonum amphibium*, *Potentilla anserina*, *Ranunculus flammula* ssp. *eu-flammula*, *Trifolium fragiferum*, *Triglochin palustre*, *Valeriana dioeca*, *Veronica comosa* and *V. scutellata*. Except *Carex fusca*, *C. oederi*, *Galium palustre* ssp. *eu-palustre* and *Potentilla anserina*, the species mentioned are of no great quantitative importance in the *Carex panicea* association. Albertson (1946, p. 134 ff.; 1950, p. 315 ff.) has pointed out that certain *Taraxacum* species of the section *Palustria* have their optimal occurrence in the *Carex panicea* association of the alvar. — With respect to other indicator species of the association, see Tab. III (pp. 111—112).

Amphibious *Carex panicea* meadows of the types described have been partly exemplified in the papers of Albertson. More or less mesic amphibious *Carex hostiana* consociations have been dealt with by Albertson 1946, Tab. 37: 1 –12. A somewhat more hydric type, poor in species, is shown by Albertson *l. c.*, 13—20. The hydric *Carex panicea* meadows have been illustrated by Albertson *op. c.* in the tables 38 and 42. A *Carex panicea - Scorpidium turgescens* sociation was exemplified by Albertson (1940, Tab. 1). The examples cited originate from the alvar areas of Västergötland, southwestern Sweden. A *Carex panicea* consociation from the Öland alvar with some affinity to the *Agrostis stolonifera* heath, mostly

with *Scorpidium lycopodioides* as bottom-layer dominant was illustrated by Albertson (1950, Tab. X). — Besides in the papers of Albertson, similar amphibious *Carex panicea* meadows on alvar soil of Öland and Västergötland have been described and shortly characterized by Sterner (1925, 1926, 1938, 1950) resp. by Du Rietz (1950 b).

Plant sociations, which perhaps are to be referred to the same association, have also been described from other Swedish limestone areas, mostly from lake shores or border-zones of swamps and marshes; from Uppland *e.g.* by Almquist (1929), Horn af Rantzien (1950), from Skåne by Waldheim (1943), and from Gotland by Du Rietz (1925), Ljungqvist (1927, 1929). Sociations of similar composition have been described also from shores of the Baltic Sea (see *e.g.* Arrhenius 1920, Almquist 1929). — Amphibious *Carex* meadows from lakes with oligotrophic detritus and humus sediments have been studied by Blomgren & Naumann (1925), Thunmark (1931), and Lillieroth (1938, 1950); floristically, they strongly differ from those described above.

Amphibious *Carex* meadows composed of low species of *Carex* and with many meadow plants as characteristic components are thus met with at Swedish lakes of quite different types. They are generally found in the upper or middle amphibious zone and are often fragmentarily developed or strongly modified by grazing. Regionally, they have been little studied and their differentiation into units of higher rank is not clear. A detailed description of such a »Parvocaricion» vegetation from a lake with eutrophic lime sediments has been given by Du Rietz & Hannerz (1939).

Examples of the composition of sociations within the *Taraxacum limnanthes - Carex panicea - Scorpidium turgescens* association.

Every example is based upon an analysis of 10 squares, each of the size of 1/4 m². The figures placed immediately after the plant names, ranging from 1 to 5 indicate the extreme values of covering according to the Hult-Sernander scale, while the figures within brackets, ranging from 10 to 100, indicate in % the number of squares, in which the plant in question was represented. For further details, see pp. 81—90.

***Carex hostiana - Ctenidium molluscum* sociation.** Alvar of Torslunda, Lenstad, wet alvar meadow in depression near deciduous forest. Mesic type, rich in species. July 24, 1949. — *Briza media* 1 (30), *Carex flacca* 1—4 (80), *C. fusca* 1 (10), *C. hostiana* 4—5 (100), *C. panicea* 1 (70), *C. pulicaris* 1 (10), *Epipactis palustris* 1—2 (100), *Equisetum palustre* 1 (20), *Eriophorum latifolium* 1 (30), *Juncus articulatus* 1—2 (70), *Linum catharticum* 1 (30), *Lotus corniculatus* 1 (40), *Molinia coerulea* 1 (20), *Pinguicula vulgaris* 2 (20), *Plantago media* 1 (20), *Potentilla erecta* 2—3 (100), *Primula farinosa* 1—2 (40), *Prunella vulgaris* 1 (60), *Rhinanthus serotinus* 1 (20), *Sesleria coerulea* 1 (30), *Viola canina* 1—2 (100), *V. pumila* 1 (40). — *Calliergonella cuspidata* 1 (60), *Campylium elodes* 1 (40), *C. polygamum* 1 (20), *C. stellatum* 1—2 (100), *Ctenidium molluscum* 2—4 (100), *Drepanocladus intermedius* 1—3 (90), *Fissidens adiantoides* 1 (40), *Mnium seligeri* 1—2 (90), *Scorpidium lycopodioides* 2—3 (60).

***Carex hostiana* - *Ctenidium molluscum* sociation.** Alvar of Stenåsa, Möckelmossen, NE part. Mesic type of average composition. July 16, 1949. — *Carex hostiana* 4—5 (100), *C. panicea* 1—2 (40), *Juncus articulatus* 1 (10), *Linum catharticum* 1 (30), *Lotus corniculatus* 1 (20), *Mentha arvensis* f. *oelandica* 1 (10), *Molinia coerulea* 1—3 (50), *Parnassia palustris* 1—2 (80), *Plantago media* 1 (10), *Potentilla erecta* 1—2 (80), *Primula farinosa* 1 (10), *Sesleria coerulea* 2 (10), *Trifolium hybridum* 1 (10), *Viola canina* 1—2 (70), *V. pumila* 1 (30). — *Bryum pseudotriquetrum* 1 (20), *Calliergonella cuspidata* 1—2 (100), *Campylium elodes* 1 (90), *C. polygamum* 1 (20), *C. stellatum* 1—2 (70), *Ctenidium molluscum* 1—4 (100), *Drepanocladus intermedius* 1 (60), *D. sendtneri* 1 (20), *Fissidens adiantoides* 1 (20), *Scorpidium lycopodioides* 1—2 (80), *S. turgescens* 1 (10).

***Carex hostiana* - *Drepanocladus sendtneri* sociation.** Alvar of Stenåsa, alvar lake at Ebbelunda. Hydric type, poor in species. July 26, 1949. — *Carex hostiana* 5 (100), *C. panicea* 1—2 (30), *Equisetum variegatum* 1 (20), *Eriophorum latifolium* 3 (10), *Galium palustre* ssp. *eu-palustre* 1 (20), *Molinia coerulea* 4 (10), *Parnassia palustris* 1 (10), *Potentilla erecta* 1—2 (40), *Succisa pratensis* 1 (30). — *Bryum neodamense* 1 (50), *B. pseudotriquetrum* 1 (20), *Calliergonella cuspidata* 1 (90), *Campylium elodes* 1 (50), *C. polygamum* 1—2 (100), *Drepanocladus intermedius* 1 (40), *D. sendtneri* 3—5 (100), *Scorpidium scorpioides* 1—3 (60).

***Carex panicea* - *Scorpidium lycopodioides* sociation.** Alvar of Stenåsa, Möckelmossen, SE part. Hydric type. July 12, 1949. — *Agrostis gigantea* 1 (30), *A. stolonifera* 1 (90), *Carex fusca* 1 (20), *C. hostiana* 1 (30), *C. oederi* 1 (40), *C. panicea* 5 (100), *Equisetum palustre* 1 (10), *Galium palustre* ssp. *eu-palustre* 1—3 (60), *Juncus articulatus* 1—2 (50), *Linum catharticum* 1 (20), *Lotus corniculatus* 1 (10), *Mentha arvensis* f. *oelandica* 2—3 (80), *Molinia coerulea* 1 (10), *Parnassia palustris* 1—2 (40), *Potentilla anserina* 1—3 (70), *Prunella vulgaris* 1 (10), *Ranunculus flammula* ssp. *eu-flammula* 1 (10), *Scirpus uniglumis* 1 (20), *Taraxacum* sp. (*Palustria*) 1 (30), *Viola pumila* 1 (40). — *Calliergonella cuspidata* 1 (30), *Campylium elodes* 1 (40), *C. polygamum* 1—2 (80), *C. stellatum* 1 (10), *Drepanocladus aduncus* 1—2 (20), *D. intermedius* 1—2 (100), *D. sendtneri* 1—2 (30), *Fissidens adiantoides* 1 (80), *Scorpidium lycopodioides* 2—4 (100), *S. turgescens* 1—2 (90).

2. The amphibious Agrostis stolonifera heaths.

On the shores of the alvar lakes and in the alvar pools, amphibious heaths — preliminarily distinguished by Albertson (1950, p. 315) as the *Agrostis stolonifera* - *Alopecurus geniculatus* - *Scorpidium turgescens* association — cover large areas of thin soil, exposed to frequent inundations. Almost at any amount of rain, the heaths become submerged; on account of the thin layer of soil (often but a few centimeters deep) they will dry up after

some hours of sunshine. Amphibious *Agrostis stolonifera* heaths are typically found in the shallow alvar depressions and in the upper and middle amphibious belt of the alvar lakes. In the thin soil areas of the lower amphibious belt, they will be met with down to the summer low-water line, but are here represented by transitional forms to the *Scirpus palustris - Littorella* marshes.

The amphibious *Agrostis stolonifera* heath is sometimes difficult to delimit against other amphibious or terrestrial associations. In the same way as the amphibious *Carex panicea* meadow is replaced by a more or less terrestrial *Sesleria-Molinia* meadow on a higher level, the amphibious *Agrostis stolonifera* heath has its terrestrial counterpart in the *Festuca ovina - Tortella* heath (*Festuca ovina - F. rubra* v. *oelandica - Tortella tortuosa* association of Albertson 1950, p. 289). Though these heath associations have a number of species in common (*e.g. Leontodon autumnalis, Sagina nodosa, Agrostis stolonifera*, and *Scorpidium turgescens*), there are generally great differences with respect to the floristic composition. The *Festuca - Tortella* heath is characterized by the presence of succulents (*e.g. Sedum*) and therophytes (*e.g. Cerastium*) in the field-layer, and by the presence of terrestrial mosses (species of *Encalypta, Hypnum cupressiforme, Thuidium abietinum*, etc.) and lichens (*e.g. Cladonia*) in the bottom-layer. The components mentioned are not at all or only exceptionally to be found in the *Agrostis* heath. The latter is furthermore distinct in the presence of some amphibious species not met with in the terrestrial heaths (*e.g. Alopecurus geniculatus, Carex oederi, Juncus alpinus* ssp. *australis* and *J. articulatus, Scirpus uniglumis, Galium palustre* ssp. *eu-palustre, Plantago tenuiflora, Potentilla anserina, Ranunculus flammula* ssp. *eu-flammula, Taraxaca Palustria, Teucrium scordium, Veronica comosa, V. scutellata, Bryum neodamense, Campylium polygamum, Drepanocladus sendtneri*, etc.). Transitional types are sometimes difficult to classify; Albertson (1950, Tab. IV) has exemplified some intermediate sociations of this type, most appropriately referred to the terrestrial heath.

Generally, the limit between terrestrial and amphibious vegetation is more easy to draw, than the limits within the amphibious vegetation. There are transitions between the amphibious heaths and the amphibious *Carex panicea* meadows as well as between the former and the amphibious *Scirpus palustris - Littorella* marshes. Generally the floristic combination scheme of amphibious

meadow and amphibious heath is so different that classification is easy. So for instance a combination in the field-layer of *Carex hostiana, Lotus corniculatus, Primula farinosa,* species of *Viola,* orchids, *Parnassia palustris, Pinguicula vulgaris, Rhinanthus serotinus, Sesleria coerulea,* and in the bottom-layer of species of *Campylium, Calliergonella, Drepanocladus intermedius, Scorpidium lycopodioides,* give strong evidence that the plant community is to be referred to the amphibious *Carex panicea* meadow, while on the contrary a combination of *Agrostis canina, Myosurus, Plantago tenuiflora, Sagina nodosa, Tortella,* and *Schistidium* suggest an amphibious *Agrostis stolonifera* heath.

Strongly hydric sociations of the amphibious *Agrostis stolonifera* heath may be difficult to delimitate from some types of amphibious *Scirpus palustris - Littorella* marsh. Comparatively dry marshes with a less hydric species composition occur sometimes in the lower amphibious zone where the soil-layer is thin, so that the risk for drying up is great. Such dry marshes often show floristic and physiognomic affinity to the *Agrostis stolonifera* heaths. The delimitation is here comparatively easy, however, on account of a number of indicator species, characteristic of the *Scirpus palustris - Littorella* marsh: *Glyceria fluitans, Scirpus palustris, Alisma plantago-aquatica, Littorella, Potamogeton gramineus* f. *terrestris, Ranunculus trichophyllus* f. *succulentus,* and *Scorpidium scorpioides.* Absence of the species mentioned and presence of *e.g. Leontodon autumnalis, Linum catharticum, Plantago tenuiflora, Prunella vulgaris, Sagina nodosa,* and *Scorpidium turgescens* suggest an *Agrostis stolonifera* heath. — The floristic composition of the association is to be seen from Tab. III (pp. 111—112).

In the *Agrostis* heath, most field-layer dominants show a considerable tolerance with respect to submersion and drought. Because of that, we do not find the same evident differentiation into a series from xeric to hydric sociations as has been met with in the amphibious *Carex panicea* meadows. The floristic composition varies a great deal, but the variation observed cannot be clearly correlated with any biotope factor. *Scorpidium turgescens* is the principal bottom-layer dominant in the entire material, while *Drepanocladus sendtneri* not seldom occurs as a subdominant species. In the field-layer *Agrostis stolonifera* is by far the most common dominant. In the temporary pools, *Alopecurus geniculatus* may be of importance too.

In the alvar, there occurs furthermore an especially poor type of amphibious *Agrostis stolonifera* heath which is devoid of bottom-layer. Albertson (1950, p. 317) has interpreted a series of analyses of this naked *Agrostis stolonifera* heath. As an expression for their poverty in species, it can be noted that Albertson found only the following vascular plants in 10 squares (percentual frequencies within brackets): *Agrostis stolonifera* (100), *Alopecurus geniculatus* (30), *Juncus alpinus* ssp. *australis* (30), *Inula britannica* (60), *Leontodon autumnalis* (10), *Linum catharticum* (10), *Mentha arvensis* f. *oelandica* (50), *Prunella vulgaris* (10), *Ranunculus flammula* ssp. *eu-flammula* (10), *Sagina nodosa* (70), and *Veronica scutellata* (60).

Amphibious *Agrostis stolonifera* heaths have been described from the alvar of Öland by Sterner (1925, 1926, 1938, 1950) and by Albertson (1950). Sociations of a similar composition have been recorded from Västergötland, southwestern Sweden, by Albertson (*e.g.* 1940, 1946) and they probably occur in Gotland too. Amphibious plant communities of meadow character with dominant *Agrostis stolonifera* are recorded from different Swedish lakes (see *e.g.* Du Rietz & Hannerz 1939) and from sea-shores. With respect to the floristic composition, they differ much from the types dealt with in the present paper. The latter are likely to be restricted to the alvar areas of Öland, Gotland and Västergötland.

Examples of the composition of sociations within the *Agrostis stolonifera* - *Alopecurus geniculatus* - *Scorpidium turgescens* association. — For explanations, see pp. 89—90.

***Alopecurus geniculatus* - *Scorpidium turgescens* sociation.** Alvar of Resmo, NE of church, temporary alvar pool. Mesic type. July 19, 1949. — *Agrostis stolonifera* 3—4 (80), *Alopecurus geniculatus* 2—5 (100), *Galium palustre* ssp. *eu-palustre* 1 (10), *Inula britannica* 1—3 (30), *Juncus articulatus* 1 (30), *Mentha arvensis* f. *oelandica* 1—3 (50), *Plantago tenuiflora* 1 (20), *Ranunculus repens* 2 (10), *Sagina nodosa* 1 (30), *Scirpus uniglumis* 2 (10), *Teucrium scordium* 1—3 (20), *Veronica comosa* 1 (30), *V. scutellata* 1—3 (70). — *Barbula convoluta* 1 (50), *Campylium polygamum* 1 (10), *Ditrichum flexicaule* 1 (50), *Drepanocladus aduncus* 1—2 (40), *D. sendtneri* 1 (30), *Scorpidium turgescens* 2—5 (100), *Tortella rigens* 1 (30). — *Chara aspera*[1] 2—3 (20).

***Carex oederi* - *Drepanocladus sendtneri* sociation.** Alvar of Stenåsa, Möckelmossen, SE part. Mesic type. July 17, 1949. — *Agrostis stolonifera* 1 (80), *Carex oederi* 4—5 (100), *C. panicea* 1 (10), *Galium palustre* ssp. *eu-palustre* 1—3 (100), *Leontodon autumnalis* 1—2 (70), *Mentha arvensis* f. *oelandica* 1—3 (60), *Molinia coerulea* 1 (20), *Potentilla anserina* 1—2 (100), *Ranunculus flammula* ssp. *eu-flammula* 1—2 (90), *Sagina nodosa* 1 (10), *Teucrium scordium* 2—4 (40). — *Bryum neodamense* 1 (30), *Calliergonella cuspidata* 1 (10), *Campylium elodes* 1 (40), *C. polygamum* 1 (60), *Ditrichum flexicaule* 1 (30), *Drepanocladus sendtneri* 2—5 (100), *Scorpidium lycopodioides* 1 (10), *S. scorpioides* 1—2 (20), *S. turgescens* 1 (80), *Tortella* sp. 1 (10).

[1] Belonging to the high-water aspect in spring. Only dead remains found at the analysis.

***Potentilla reptans - Drepanocladus sendtneri* sociation.** Alvar of Gårdby, ESE of the Lenstad village, temporary alvar pool. Mesic type. July 22, 1949. — *Agrostis stolonifera* 1—2 (70), *Carex oederi* 1—4 (100), *C. panicea* 1 (10), *Galium palustre* ssp. *eu-palustre* 1—3 (100), *Juncus articulatus* 1 (30), *Leontodon autumnalis* 1—2 (60), *Mentha arvensis* f. *oelandica* 1—2 (90), *Molinia coerulea* 1 (10), *Potentilla anserina* 1—2 (40), *P. reptans* 5 (100), *Ranunculus flammula* ssp. *eu-flammula* 1—2 (40), *R. repens* 1—3 (30), *Scirpus uniglumis* 1—3 (30), *Teucrium scordium* 2—4 (80), *Veronica scutellata* 1 (20). — *Barbula convoluta* 1 (10), *B. rigidula* 1 (10), *Bryum neodamense* 1 (90), *Calliergonella cuspidata* 1 (10), *Campylium polygamum* 1 (50), *Drepanocladus sendtneri* 2—5 (100), *Scorpidium turgescens* 1—5 (80).

***Potentilla anserina - Scorpidium turgescens* sociation.** Alvar of Gårdby, ESE of the Lenstad village, temporary alvar pool. Mesic type. July 22, 1949. — *Agrostis stolonifera* 1—3 (90), *Carex oederi* 1—2 (80), *Galium palustre* ssp. *eu-palustre* 1—4 (80), *Leontodon autumnalis* 1 (10), *Mentha arvensis* f. *oelandica* 1 (20), *Potentilla anserina* 5 (100), *P. reptans* 1—2 (50), *Ranunculus flammula* ssp. *eu-flammula* 1—2 (40), *R. repens* 1 (10), *Scirpus uniglumis* 1—2 (40), *Teucrium scordium* 1—5 (70). — *Barbula rigidula* 1 (60), *Bryum neodamense* 1 (20), *B. pseudotriquetrum* 1 (10), *Calliergonella cuspidata* 1 (10), *Campylium elodes* 1 (30), *C. polygamum* 1 (20), *C. stellatum* 1 (10), *Ditrichum flexicaule* 1 (20), *Drepanocladus aduncus* 1 (10), *D. sendtneri* 1—2 (50), *Schistidium apocarpum* 1 (10), *Scorpidium lycopodioides* 1 (10), *S. turgescens* 2—5 (100), *Tortella rigens* 1 (50).

***Agrostis stolonifera - Scorpidium turgescens* sociation.** Alvar of Resmo, Möckelmossen, SW part. Hydric type. July 15, 1949. — *Agrostis stolonifera* 3—5 (100), *Alisma plantago-aquatica* 1 (10), *Carex oederi* 1—4 (50), *C. panicea* 3 (10), *Echinodorus ranunculoides* 1 (10), *Galium palustre* ssp. *eu-palustre* 2—3 (60), *Juncus alpinus* ssp. *australis* 3 (10), *J. articulatus* 1—3 (80), *Lythrum salicaria* 1 (10), *Mentha arvensis* f. *oelandica* 1—3 (70), *Ranunculus flammula* ssp. *eu-flammula* 1—2 (50). — *Bryum neodamense* 1 (60), *B. pseudotriquetrum* 1 (10), *B.* sp. 1 (10), *Campylium elodes* 1 (20), *C. polygamum* 1 (40), *Drepanocladus intermedius* 1 (10), *D. sendtneri* 1—2 (50), *Scorpidium lycopodioides* 1 (20), *S. scorpioides* 1 (20), *S. turgescens* 2—5 (100). — *Chara aspera*[1] 1—5 (100).

***Carex panicea - Scorpidium turgescens* sociation.** Alvar of Resmo, W of Möckelmossen, temporary alvar pool. Mesic type. July 20, 1949. — *Agrostis stolonifera* 1—2 (100), *Carex panicea* 4—5 (100), *Galium palustre* ssp. *eu-palustre* 2—4 (100), *Inula britannica* 1—2 (20), *Juncus alpinus* ssp. *australis* 1—2 (70), *J. articulatus* 1 (50), *J. compressus* 1 (10), *Mentha arvensis* f. *oelandica* 1—3 (60), *Ranunculus flammula* ssp. *eu-flammula* 1 (30), *Sagina nodosa* 1 (20), *Scirpus uniglumis* 1 (40). — *Bryum neodamense* 1 (20), *B. pseudotriquetrum* 1 (10), *Calliergonella cuspidata* 1 (30), *Campylium polygamum* 1 (60), *Drepanocladus aduncus* 1—2 (20), *D. sendtneri* 2—3 (70), *Scorpidium turgescens* 2—5 (100), *Tortella* sp. 1 (10).

[1] Belonging to the high-water aspect in spring. Only dead remains found at the analysis.

3. The amphibious Scirpus palustris - Littorella marshes.

Two associations are of considerable importance in the lower amphibious belt of the alvar lakes, *viz.* the *Scirpus palustris - Littorella* marsh and the *Carex elata* swamp. A third association is to be added, the amphibious *Phragmites* reed-swamp, which is only very fragmentarily developed. These associations are generally absent from the small temporary pools.

The *Scirpus palustris - Littorella* marshes have a characteristic physiognomy and floristic composition, and are generally easy to delimit from other amphibious associations of the alvar. Transitional types are rather frequent, however. The following components characteristic of the *Scirpus palustris - Littorella* marshes, are not at all or only occasionally to be met with in those amphibious alvar associations which have already been dealt with: *Echinodorus ranunculoides, Glyceria fluitans, Littorella uniflora, Potamogeton gramineus* f. *terrestris, P. natans* f. *terrestris, Ranunculus trichophyllus* f. *succulentus, Scirpus palustris,* and *Triglochin palustre.* Many terric or mesic components which are common to the *Agrostis stolonifera* heath and the *Carex panicea* meadow are furthermore not to be observed in the marshes, *e.g. Inula britannica, Leontodon autumnalis, Molinia coerulea, Sagina nodosa,* species of *Taraxaca Palustria,* and *Teucrium scordium.* The following components of the *Carex panicea* meadow are indicator species not entering the *Agrostis stolonifera* heath or the *Scirpus palustris - Littorella* marsh: *Campylium stellatum, Cardamine pratensis, Carex hostiana, Ctenidium molluscum, Drepanocladus intermedius, Epipactis palustris, Lotus corniculatus, Pinguicula vulgaris, Polygala amarella, Potentilla erecta, Primula farinosa,* etc. The *Agrostis stolonifera* heaths, finally, are characterized by some species which are not to be found in the *Scirpus palustris - Littorella* marshes or in the *Carex panicea* meadows: species of *Barbula, Plantago tenuiflora, Ranunculus repens, Schistidium apocarpum, Tortella rigens,* and some others. The differential indicator species of the *Scirpus palustris - Litorella* marshes against the amphibious *Carex elata* swamps and against the amphibious reed-swamps are enumerated in the sections devoted to those plant communities. It is furthermore to be pointed out that the aquatic *Littorella-Echinodorus* union does not differ from its amphibious more-layered counterpart, the *Scirpus palustris - Littorella uniflora - Scorpidium scorpioides* association by any indicator

Fig. 3. Möckelmossen, southeastern part. Shallow lagoon (with *Littorella* society and *Chara aspera* society) surrounded by amphibious *Scirpus palustris - Littorella* marsh (in the foreground holes with *Chara aspera*). July 16, 1949. Photo: the writer.

species among the isoetids. If all aquatic life-forms are combined, however, we get some good aquatic indicator species (*e.g. Chara aspera, Myriophyllum alterniflorum, Potamogeton pectinatus,* etc.). The *Scirpus-Littorella-Scorpidium* association differs furthermore from the *Littorella-Echinodorus* union by the presence of a number of terrestrial and amphibious components, *viz. Agrostis stolonifera, Carex oederi, Eriophorum latifolium, Galium palustre* ssp. *eu-palustre, Mentha arvensis* f. *oelandica, Myosotis laxa* ssp. *caespitosa, Potentilla anserina, Scirpus pauciflorus, Triglochin palustre,* etc. — With respect to the floristic composition and the indicator species of this association, see furthermore Tab. III (pp. 111—112).

Contrary to the other hydric amphibious associations of the alvar lakes which are »swamps» (or »fens»), this association is a typical »marsh», that is, it has a mineral or muddy basis, contrasting to the peat-basis of the fens (see Pearsall 1918, and later British ecologists). The *Scirpus palustris - Littorella* marsh is almost exclusively found on lime gyttja, and requires a sufficiently deep layer of this sediment. The majority of the species constituting this association are rather sensitive to a drying up of their substrate.

Albertson (1950, p. 315) has classified similar plant communi-

ties as the *Carex oederi - Scirpus palustris - Scorpidium scorpioides* association. The writer prefers to term this plant community the *Scirpus palustris - Littorella uniflora - Scorpidium scorpioides* association. The name of the association is of course only of minor importance; it is more important to realize that neither *Carex oederi* nor *Littorella uniflora* are to be found in all the different types of this marsh.

Scorpidium scorpioides, Drepanocladus aduncus and *D. sendtneri* are the principal dominants of the bottom-layer. *Bryum neodamense, Campylium elodes,* and *C. polygamum* are found in single individuals or tufts in most squares analysed.

In the field-layer *Carex fusca, C. oederi, Glyceria fluitans, Juncus articulatus, Littorella uniflora,* and *Scirpus palustris* are the most important dominants. The last mentioned is one of the most frequent components of the association, and also one of its best differential species. In disputable cases, it is often preferable to draw the association limit according to its occurrence.

Albertson (1950, pp. 319—320), has pointed out the peculiar position of the *Littorella* community of the alvar: »Die Litorella-Sozietät ist infolge des markanten Einschlages oligotropher westeuropäischer Arten ein auf dem Gross-Alvar fast einzigartiger Verein». The general phytogeographical character of the sociation (with *Echinodorus ranunculoides, Apium inundatum,* and in the aquatic vegetation, *Myriophyllum alterniflorum*) is in contrast with the other principal groups of the alvar vegetation, the arctic-alpine mountain component, the southeastern steppe component and the southern lithic component. The species enumerated are furthermore remarkable in being restricted to aquatic localities with oligotrophic sediments, irrespective of the varying Ca content of the latter. The latter problem has been dealt with at some length by Roll (1939, with experiments; cf. also Moor 1936 and Tüxen 1937).

The *Scirpus palustris - Littorella uniflora - Scorpidium scorpioides* association is probably restricted to the alvar areas of Öland and Gotland. From central Gotland, Ljungqvist (1927, pp. 322—327) has described marshes of a similar though not identical composition and physiognomy. The association is not found in the alvar areas of Västergötland. Albertson (1946, p. 140 and Tab. 45) has described a *Carex fusca* consociation, which is perhaps an alternative equivalent to the *Scirpus palustris - Littorella* marshes, but which clearly differs from the latter.

Fig. 4. Möckelmossen, southeastern part. Details from the shores of the shallow lagoon, fig. 3. — Left fig. Flowering *Echinodorus* sociation in mat of dead or dying *Chara aspera*. — Right fig. In centre depression with dead *Chara aspera*, surrounded by *Littorella* sociation. July 16, 1949. Photo: the writer.

In the prevalence of *Scorpidium scorpiodes* and *Drepanocladus sendtneri* in the bottom-layer and in the presence of a number of exacting amphibious basibionts in the field-layer, the *Scirpus palustris* - *Littorella* marshes resemble the extreme rich fens (the Eu-Scorpidium suballiance) of Du Rietz and other Swedish paludologists (see Du Rietz' comprehensive paper of 1949, and for illustrative examples *e.g.* Waldheim & Weimarck 1943 and Witting esp. 1947). There are certain important differences, however.

The ecological equivalents of the *Scirpus palustris* - *Littorella* marshes are to be searched for elsewhere. They should be looked for in a group of freshwater marsh communities developed in exposed shore sections of the lower amphibious zone in a number of Swedish lakes. The detailed composition of such a plant community was for the first time studied in detail by Du Rietz and Hannerz in their monograph of Lake Tåkern, Central Sweden (Du Rietz & Hannerz 1939). In Tåkern these sociations are dominated and characterized by *Scirpus acicularis* and *S. palustris*.

»Der »Land-*Scirpus*-Horizont» des Tåkern entspricht der untersten der drei Unterstufen, in die Blomgren & Naumann (1925) sowie Thunmark (1931, 1938) ihr »Eulitoral» an den sauren oligotrophen Seen der südschwedischen Landhöhe eingeteilt haben. *Scirpus palustris* kommt auch dort vor, *Scirpus acicularis* ist aber durch *Lobelia Dortmanna* und *Litorella uniflora* ersetzt, und die Unterstufe wurde in den Feldnotizen Du Rietz'

aus Småland und Halland manchmal als »die Land - *Lobelia* - Stufe» oder »die *Isoetes* - freie *Lobelia* - *Litorella* - Stufe» bezeichnet. Bei Lilla Ullevifjärden (Mälaren, vergl. Wærn 1939 a) wird die entsprechende Unterstufe (nach Notizen von Du Rietz vom 31.V. 1939) von einem *Litorella* - *Scirpus acicularis* - *Ranunculus reptans* - Horizont gebildet.» (Du Rietz & Hannerz *op. c.*, p. 35).

The observations of Du Rietz and Hannerz have a general applicability to Swedish lakes. The writer has found an amphibious *Scirpus palustris* zone in a number of various lakes. Though the floristic composition varies the zone presents a rather uniform physiognomy, with the field-layer divided into two *étages* with medium tall culms of *Scirpus palustris*, *S. uniglumis* or *S. mamillatus* in the upper sub-layer, and low, only some few centimeters high individuals of *Scirpus acicularis*, *S. parvulus*, *Lobelia*, *Littorella*, etc. in the lower sub-layer. The latter *étage* replaces a bottom-layer of mosses, which is in general fragmentary or absent. The *Scirpus palustris* zone is restricted to exposed shores; in sheltered shore sections this marsh is expelled by *Carex elata* swamps and amphibious reed-swamps. On the whole, marshes of this type have a slight competitive power. They seem to be bound to a soil kept free from other vegetation by a not too strong ice erosion. As a further characteristic feature may be mentioned their absence or slight development in lakes with considerable production of humus sediments. Then the shore is often peaty and loose, which is not favourable for the *Scirpus palustris* marsh; a more or less fragmentary occurrence of *Scirpus mamillatus* swamp is often observed in such localities.

Although amphibious marshes of this type have been comparatively little studied, it seems evident that they show an interesting differentiation in communities of high rank. It is at least possible to distinguish a *Scirpus palustris* - *S. acicularis* - *Drepanocladus exannulatus* association in lakes with eutrophic sediments of the usual type, and a *Scirpus palustris* - *S. acicularis* - *Scorpidium scorpiodes* association in lakes with eutrophic lime sediments. Almquist (1929, p. 82) has given some examples on the former type, the latter was studied in detail by Du Rietz & Hannerz (1939). Their counterparts in lakes with oligotrophic sediments are the *Scirpus palustris* - *Lobelia dortmanna* - *Drepanocladus fluitans* association and the *Scirpus palustris* - *Littorella uniflora* - *Scorpidium scorpioides* association. The latter is exclusively found in lakes with lime sediments poor in nutrition. Many examples on the former type have been given from the Aneboda lakes, *e.g.* by Blomgren & Naumann (1925), Thunmark (1931) and Lillieroth (1938, 1950). Also on brackish water shores of the Baltic Sea, we meet the same type of vegetation, here generally developed as a *Scirpus uniglumis* v. *fennicus* - *S. parvulus* - *Campylium polygamum* association.

Examples of the composition of sociations within the *Scirpus palustris* - *Littorella uniflora* - *Scorpidium scorpioides* association. For explanations see pp. 89—90.

***Agrostis stolonifera - Scorpidium scorpioides* sociation.** Alvar of Resmo, Möckelmossen, western shore. Mesic transitional type to the *Agrostis stolonifera* heath. July 16, 1949. — *Agrostis stolonifera* 3—5 (100), *Alisma plantago-aquatica* 1 (20), *Carex oederi* 1 (20), *Echinodorus ranunculoides* 1—3 (80), *Juncus alpinus* ssp. *australis* 1 (30), *J. articulatus* 1—3 (90), *Littorella uniflora* 1 (10), *Lythrum salicaria* 1 (10), *Mentha arvensis* f. *oelandica* 1 (30), *Myosotis laxa* ssp. *caespitosa* 1 (10), *Potamogeton gramineus* f. *terrestris* 1 (40), *Ranunculus flammula* ssp. *eu-flammula* 1 (20), *R. trichophyllus* f. *succulentus* 1 (10), *Scirpus palustris* 1—2 (40). — *Bryum neodamense* 1 (90), *Campylium polygamum* 1 (30), *Drepanocladus sendtneri* 1 (80), *Scorpidium scorpioides* 3—5 (100), *S. turgescens* 1 (10). — *Chara aspera*[1] 5 (100).

***Juncus articulatus* sociation.** Alvar of Gårdby, temporary alvar pool ESE of the Lenstad village. Mesic type. July 22, 1949. — *Carex oederi* 1—3 (80), *Eriophorum latifolium* 1 (10), *Juncus articulatus* 2—3 (100), *Scirpus palustris* 1—2 (100), *S. pauciflorus* 1 (10), *S. uniglumis* 1—2 (50), *Triglochin palustre* 2 (20). — *Preissia quadrata* 2 (10), *Scorpidium scorpioides* 1 (30). — *Chara aspera*[1] 4—5 (100).

***Potentilla anserina - Scorpidium scorpioides* sociation.** Alvar of Gårdby, temporary alvar pool ESE of the Lenstad village. Mesic transitional type to the *Agrostis stolonifera* heath. July 22, 1949. — *Agrostis stolonifera* 1—2 (70), *Galium palustre* ssp. *eu-palustre* 3—4 (100), *Littorella uniflora* 1 (10), *Potentilla anserina* 4—5 (100), *Ranunculus flammula* ssp. *eu-flammula* 1 (30), *Scirpus palustris* 4—5 (100). — *Bryum neodamense* 1 (90), *Drepanocladus sendtneri* 1 (30), *Scorpidium scorpioides* 5 (100). — *Chara aspera*[1] 1—2 (40).

***Carex fusca* sociation.** Alvar of Gårdby, temporary alvar pool ESE of the Lenstad village. Mesic type. July 22, 1949. — *Carex fusca* 4—5 (100), *C. oederi* 1 (20), *Equisetum variegatum* 1 (10), *Galium palustre* ssp. *eu-palustre* 1—2 (100), *Juncus articulatus* 1 (30), *Potentilla anserina* 1—4 (100), *Scirpus palustris* 1—3 (60). — *Scorpidium scorpioides* 1 (10). — *Chara aspera*[1] 1—3 (40).

***Carex oederi - Scorpidium scorpioides* sociation.** Alvar of Gårdby, temporary alvar pool ESE of the Lenstad village. Mesic type. July 22, 1949. — *Carex fusca* 1 (10), *C. oederi* 3—4 (100), *C. panicea* 1 (10), *Galium palustre* ssp. *eu-palustre* 1—2 (100), *Juncus articulatus* 1—3 (70), *Mentha arvensis* f. *oelandica* 1 (40), *Ranunculus flammula* ssp. *eu-flammula* 2—3 (30). — *Bryum neodamense* 1 (100), *B. pseudotriquetrum* 1 (10), *Campylium elodes* 1 (60), *C. polygamum* 1—2 (100), *C. stellatum* 1 (10), *Drepanocladus intermedius* 1 (30), *D. sendtneri* 1 (10), *Preissia quadrata* 2—3 (20), *Scorpidium scorpioides* 3—4 (100). — *Chara aspera*[1] 2—3 (90).

***Littorella uniflora - Scorpidium scorpioides* sociation.** Alvar of Stenåsa, Möckelmossen, eastern shore. Hydric type. July 16, 1949. — *Agrostis stolo-*

[1] Belonging to the high-water aspect in spring. Only dead remains were found at the analysis.

nifera 1—2 (40), *Echinodorus ranunculoides* 1—3 (60), *Galium palustre* ssp. *eu-palustre* 1 (10), *Juncus articulatus* 1—2 (30), *Littorella uniflora* 4—5 (100), *Mentha arvensis* f. *oelandica* 1 (10), *Ranunculus flammula* ssp. *eu-flammula* 1—4 (20), *R. trichophyllus* f. *succulentus* 1 (30), *Scirpus palustris* 2—4 (70), *S. uniglumis* 1 (10). — *Bryum neodamense* 1 (40), *B. pseudotriquetrum* 1 (10), *Campylium polygamum* 1 (30), *Drepanocladus sendtneri* 1—2 (60), *Scorpidium scorpioides* 3—5 (100). — *Chara aspera*[1] 2—3 (50).

***Littorella uniflora* sociation.** Alvar of Stenåsa, Möckelmossen, eastern shore. Hydric type. July 16, 1949. — *Alisma plantago-aquatica* 1 (10), *Echinodorus ranunculoides* 1—3 (70), *Equisetum fluviatile* 2 (10), *Glyceria fluitans* 1 (10), *Juncus articulatus* 1 (40), *Littorella uniflora* 4—5 (100), *Ranunculus trichophyllus* f. *succulentus* 1 (20), *Scirpus palustris* 1—3 (60), *S. uniglumis* 1 (20). — *Scorpidium scorpioides* 1 (20). — *Chara aspera*[1] 1—3 (100).

***Scirpus palustris* sociation.** Alvar of Resmo, Möckelmossen, southernmost part. Hydric type. July 17, 1949. — *Echinodorus ranunculoides* 1 (10), *Equisetum variegatum* 1 (10), *Juncus alpinus* ssp. *australis* 1—2 (20), *J. articulatus* 1—4 (70), *Menyanthes trifoliata* 2—4 (20), *Potamogeton gramineus* f. *terrestris* 1—4 (60), *Ranunculus flammula* ssp. *eu-flammula* 4 (10), *Scirpus palustris* 3—5 (100), *S. tabernaemontani* 1—2 (30), *S. uniglumis* 1—2 (40). — *Scorpidium scorpioides* 1 (10). — *Chara aspera*[1] 3—5 (100).

***Scirpus tabernaemontani* sociation.** Alvar of Resmo, Möckelmossen, southernmost part. Hydric type. July 17, 1949. — *Echinodorus ranunculoides* 3 (10), *Equisetum fluviatile* 3 (10), *Juncus alpinus* ssp. *australis* 1 (40), *J. articulatus* 2—3 (90), *Potamogeton gramineus* f. *terrestris* 1—2 (100), *Ranunculus flammula* ssp. *eu-flammula* 1 (10), *Scirpus palustris* (including hybrids with *S. uniglumis*) 1—2 (80), *S. tabernaemontani* 2—5 (100), *S. uniglumis* 1—2 (50). — *Chara aspera*[1] 3—5 (100).

***Eriophorum angustifolium* - *Scorpidium scorpioides* sociation.** Alvar of Resmo, Möckelmossen, southernmost part. Hydric type. July 19, 1949. — *Carex fusca* 1 (20), *C. oederi* 1 (10), *Echinodorus ranunculoides* 1 (10), *Equisetum fluviatile* 1—2 (80), *E. variegatum* 1 (20), *Eriophorum angustifolium* 2—5 (100), *Juncus articulatus* 1—3 (90), *Potamogeton gramineus* f. *terrestris* 2 (10), *Scirpus palustris* 2—4 (60), *S. uniglumis* 1—2 (40). — *Bryum neodamense* 1 (30), *Campylium polygamum* 1 (10), *Scorpidium scorpioides* 2—5 (100). — *Chara aspera*[1] 1—5 (100).

***Equisetum fluviatile* sociation.** Alvar of Resmo, Möckelmossen, southernmost part. Hydric type. July 19, 1949. — *Carex fusca* 1—3 (30), *C. oederi* 1 (20), *Equisetum fluviatile* 4—5 (100), *Eriophorum angustifolium* 3—4 (100), *Juncus articulatus* 1—3 (80), *Scirpus palustris* 1—2 (70). — *Scorpidium scorpioides* 1 (20). — *Chara aspera*[1] 3—5 (40).

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[1] Belonging to the high-water aspect in spring. Only dead remains were found at the analysis.

***Menyanthes trifoliata* sociation.** Alvar of Resmo, Möckelmossen, southernmost part. Hydric type. July 19, 1949. — *Carex fusca* 1 (10), *Equisetum fluviatile* 1—2 (50), *Eriophorum angustifolium* 1—2 (20), *Juncus articulatus* 1—2 (60), *Menyanthes trifoliata* 3—5 (100), *Potamogeton gramineus* f. *terrestris* 1 (20), *Scirpus palustris* 1—3 (70), *S. tabernaemontani* 1 (30). — *Scorpidium scorpioides* 1 (10). — *Chara aspera*[1] 3—5 (100).

4. The amphibious Carex elata swamps.

As stated above, the local distribution of the *Carex elata* swamp in the alvar lakes is to some degree correlated with the occurrence of peat. At present these deposits are mainly found in the deepest parts of the basins, but have been eroded from the shores. Where such is the case — as for instance in Lake Möckelmossen — the *Carex elata* swamp generally forms an island or a system of islands in the middle of the lake, surrounded by open water on all sides. This is one of the most spectacular aspects of many alvar lakes. They differ in this respect topographically from most lakes of the Swedish mainland. In some alvar lakes, however (*e.g.* the lake at Fröslunda) the *Carex elata* swamp is found on wet alvar soil rich in humus. They are then covering marginal parts of the lake.

The *Carex elata* swamps of the alvar are no suitable objects of a vegetation analysis. They are represented by an impoverished variant of an association, which is a characteristic lake-border community in Swedish lakes with eutrophic sediments. This association, preliminarily termed the *Carex elata - C. appropinquata - Scorpidium scorpioides* association, is generally rich in exacting species. Only few of them are found in the alvar lake variant, which will be shortly described below.

In the field-layer, *Carex elata* is almost the only dominant species. It is true that *Menyanthes*, *Glyceria fluitans* or *Carex lasiocarpa* may dominate very locally too; in such cases there is a characteristic alternation between *Carex elata* tussocks and patches of other sociations. It is probably more preferable to regard these communities as association-complexes of *Carex elata* swamp and amphibious reed-swamp. The other components are generally restricted to the lower marginal decaying parts of the *Carex elata* tussocks. As

[1] Belonging to the high-water aspect in spring. Only dead remains were found at the analysis.

field-layer species in the alvar lakes have been observed: *Alisma plantago-aquatica, Caltha palustris, Carex lasiocarpa, C. oederi, Equisetum fluviatile, Galium palustre* ssp. *eu-palustre, Glyceria fluitans, Juncus articulatus, Lysimachia vulgaris, Lythrum salicaria, Mentha aquatica, Menyanthes trifoliata, Myosotis laxa* ssp. *caespitosa, Phragmites communis, Polygonum amphibium* f. *terrestre, Potamogeton gramineus* f. *terrestris, Potentilla anserina, Ranunculus flammula* ssp. *eu-flammula, R. trichophyllus* f. *succulentus, Scirpus palustris, S. uniglumis, Typha latifolia,* and *Veronica scutellata.* As bottom-layer components have been recorded: *Campylium elodes, C. polygamum, Drepanocladus aduncus, D. intermedius, D. sendtneri, Scorpidium lycopodioides,* and *S. scorpioides,* etc. It should be noted that the bottom-layer is generally absent or only slightly developed. This is certainly correlated with slow humification of the dead leaves and sheaths of *Carex elata,* which form a less favourable substrate for the bryophytes. Corresponding conditions are to be observed in the *Cladium mariscus* swamps too.

From a floristic point of view, the *Carex elata* swamps are more closely allied to the amphibious reed-swamps than to any other amphibious community in the alvar lakes. As the reed-swamps are only fragmentarily developed here, differential species between the two associations generally present in the alvar lakes are not easily given. In the amphibious reed-swamps of the Swedish mainland, however, the luxuriantly developed bottom-layer with *Calliergon giganteum, C. megalophyllum, Sphagnum obtusum, Cinclidium stygium,* etc., the thickets of *Solanum dulcamara* and *Galium trifidum,* and the regular presence of *Malaxis paludosa, Corallorhiza, Comarum,* etc., delimit them from the *Carex elata* swamps. Besides, the physiognomy of the reed-quagmires and that of the *Carex elata* tussocks is of course very different (for further details, see the following section).

The differences are much greater between the *Carex elata* swamps and the other amphibious associations. It is not necessary to make up lists of indicator species here; reference is made to the above list of the species found in the *Carex elata* swamps and to Tab. III. There is a considerable number of hydric species, common to the *Carex elata* swamp and to the *Scirpus palustris - Littorella* marsh, which do not enter the *Carex panicea* meadow or the *Agrostis stolonifera* heath. Likewise, many mesic species observed in one of the latter plant communities or common to both of them, are not

to be found in the hydric associations. Among the field-layer components observed in the alvar-lake variant of the *Carex elata* swamp, especially *Caltha, Lysimachia vulgaris, Mentha aquatica,* and *Typha latifolia* are important as having not or only exceptionally been met with in the *Scirpus palustris - Littorella* marsh. The latter association is characterized by a number of species not to be found in the former, *e.g. Equisetum variegatum, Echinodorus, Littorella,* and *Scirpus uniglumis.*

Plant communities dominated by *Carex elata* are frequent on wet soil in South and Central Sweden. They are generally termed »Magnocaricion elatae» in Scandinavian and Central European ecological literature (originally introduced by Koch 1926). From a sociological point of view, this term covers a heterogeneous assemblage of plant communities. Scandinavian types are rather insufficiently investigated. Preliminarily, at least two associations can be distinguished: the *Carex elata - C. appropinquata-Scorpidium scorpioides* association, characterized by many exacting basibionts in the field- and bottom-layers, and found on eutrophic soil, and the *Carex elata - C. diandra - Drepanocladus exannulatus* association with a less exacting species composition, found on soils more poor in nutrition. Both contain sociations with and without bottom-layer, the latter types are most frequent. The *Carex elata* swamp described from the alvar lakes of Öland are to be considered as an impoverished variant of the *Carex elata - Scorpidium* association. In the Swedish mainland, this plant community is characterized by many species, not recorded from the alvar lakes, *e.g. Carex paniculata, C. pseudocyperus, Epilobium hirsutum, Galium uliginosum, Juncus subnodulosus,* etc., while in the bottom-layer *Calliergonella cuspidata, Drepanocladus aduncus, D. sendtneri, Mnium seligeri, Scorpidium scorpioides,* etc. are the most characteristic components. In the *Carex elata - C. diandra - Drepanocladus exannulatus* association, *Carex lasiocarpa, C. rostrata, Myrica gale,* various *Sphagna,* etc. are often characteristic components besides the denominating species. — Lake border communities with dominating *Carex elata* have been described *e.g.* from Östergötland and Närke (Du Rietz & Hannerz 1939, Stålberg 1939: both excellent descriptions of the rich, basibiontic type) and from Uppland (Almquist 1929, Horn af Rantzien 1950). See also Ljungqvist 1919 (Gotland) and Waldheim & Weimarck 1943 (Skåne).

In the alvar lakes, only one sociation is of importance: the *Carex elata* sociation without or with a slightly developed bottom-layer. The following example is taken from the shore of the alvar lake at Fröslunda, and illustrates the average hydric type. July 26, 1949. (Explanation pp. 89—90.) — *Caltha palustris* 1 (20), *Carex elata* 3—5 (100), *Juncus articulatus* 1 (10), *Lythrum salicaria* 1 (20), *Mentha aquatica* 1—2 (50), *Potamogeton gramineus* f. *terrestris* 1 (10). — *Campylium elodes* 1 (70), *C. polygamum* 1 (60), *Drepanocladus intermedius* 1 (10), *D. sendtneri* 1 (30), *Scorpidium lycopodioides* 1 (40), *S. scorpioides* 1 (50).

Tab. III. The principal lake-shore components in the vegetation of the Öland alvar and their occurrence in the amphibious associations: the *Carex panicea* meadow (I), the *Agrostis stolonifera* heath (II), the *Scirpus palustris - Littorella* marsh (III) and the *Carex elata* swamp (IV).

Fat-faced type = especially characteristic and useful indicator species of one or more of the associations; D = observed as a dominant within the association; + = regular occurrence; (+) = observed but of one or another reason considered as alien to the association.

	I	II	III	IV		I	II	III	IV
Agrostis canina		+			*Gnaphalium uliginosum*	+	+		
A. gigantea	+				***Herminium monorchis***	+			
A. stolonifera	+	D	D		***Hydrocotyle vulgaris***	+			
Alisma plantago-aquatica		(+)	+	+	*Inula britannica*	+	+	(+)	
Alopecurus geniculatus	+	D	+		*Juncus alpinus* ssp. *australis*	+	D	D	
Apium inundatum			+		*J. articulatus*	+	D	D	+
Braya supina		(+)			*J. bufonius*	(+)	+	(+)	
Briza media	+				*J. bulbosus* f. *terrestris*			D	
Caltha palustris	+		(+)	+	*J. compressus*		+	(+)	
Carex elata				D	*J. ranarius*		+	(+)	
C. flacca	D				***Leontodon autumnalis***	+	+		
C. fusca	D	+	D		*Linum catharticum*	+	+		
C. hostiana	D				***Littorella uniflora***			D	
C. lasiocarpa			+	+	***Lotus corniculatus***	+			
C. oederi	D	D	D	+	*Lysimachia vulgaris*				+
C. panicea	D	D	+		*Lythrum salicaria*	+	+	+	+
C. pulicaris	+				*Mentha aquatica*	(+)			+
Cardamine pratensis	+				*M. arvensis* f. *oelandica*	+	D	+	
Centaurium pulchellum		+			***Menyanthes trifoliata***			D	+
C. vulgare		+			*Molinia coerulea*	D	+		
Deschampsia caespitosa	(+)				*Myosotis laxa* ssp. *caespitosa*	+		+	+
Draba verna		(+)			***Myosurus minimus***		+	(+)	
Echinodorus ranunculoides		(+)	D		*Odontites rubra*	+	+		
Epipactis palustris	+				***Ophrys insectifera***	+			
Equisetum fluviatile			D	+	***Orchis incarnatus***	+			
E. palustre	+				*O. militaris*	(+)			
E. variegatum	(+)	+	+		***Parnassia palustris***	+			
Eriophorum angustifolium			D		*Pedicularis palustris*	(+)		(+)	
E. latifolium	+			+	*Phragmites communis*				+
Euphrasia brevipila	+				***Pinguicula vulgaris***	+			
E. »stricta»	+	+			*Plantago major* ssp. *intermedia*	+	+		
Galium palustre ssp. *eu-palustre*	D	D	+	+	*P. maritima*	+	+		
G. uliginosum	+				*P. media*	+			
Glyceria fluitans			D	+	***P. tenuiflora***		+		

	I	II	III	IV		I	II	III	IV
Polygala amarella	+				***Scirpus palustris***			D	+
Polygonum amphibium	+	+	+	+	*S. pauciflorus*	+	+	+	
P. aviculare		+			*S. planifolius*	+			
Potamogeton gramineus* f. *terrestris			D	+	*S. tabernaemontani*			D	
P. natans* f. *terrestris			+		*S. uniglumis*	+	+	D	+
Potentilla anserina	D	D	D	+	***Sesleria coerulea***	+			
P. erecta	+				*Succisa pratensis*	+	(+)		
P. reptans	D	D	(+)		*Taraxacum* (*Palustria*) spp.	+	+		
Primula farinosa	+				***Teucrium scordium***	D	D		
Prunella vulgaris	+	+			*Thalictrum flavum*	(+)			
Ranunculus flammula ssp. *eu-flammula*	D	+	D	+	***Trifolium fragiferum***	+			
R. repens		+			*T. hybridum*	(+)			
R. trichophyllus* f. *succulentus		(+)	+	+	***T. repens***	+			
Rhinanthus serotinus	+				*Triglochin palustre*	+		+	
Rumex acetosa	+				*Typha latifolia*				+
R. acetosella		(+)			*Valeriana dioeca*	+			
Sagina nodosa	(+)	+			*Veronica comosa*	(+)	+	+	
Schoenus ferrugineus	(+)				*V. scutellata*	+	+	+	+
					Vicia hirsuta	(+)	(+)		
					Viola canina	+			
					V. pumila	+			

The table is exclusively based upon general lists from the various associations made up by the writer in the field. The lists are not complete; some species are likely to have been overlooked. Only vascular plants have been included; the lists of mosses outside the square quadrats are not sufficient to show the distribution except for dominants and subdominants. — The amphibious reed-swamp has been left out; this fragmentary association cannot be directly compared with the other associations listed in a table like this.

5. The amphibious reed-swamps.

Amphibious reed-swamps are fragmentarily developed in the alvar lakes and cover only small areas there. Because of that they will be only shortly discussed.

In Möckelmossen the amphibious reed-swamps as well as the *Carex elata* swamps are restricted to the lower amphibious belt, and are found mostly on peat or loose water-drenched soil rich in humus. They have been observed together with the latter association in the deep central part of the lake (with *Menyanthes trifoliata*, *Phragmites communis*, *Polygonum amphibium* f. *terrestre*, *Equisetum fluviatile*, and *Galium palustre* as field-layer dominants; bottom-layer almost entirely absent) and as patches on the shores, especially

Fig. 5. Möckelmossen, southwestern part. — Left fig. Thin-soil area covered by a light *Agrostis stolonifera* heath (*Agrostis-Nostoc* sociation). July 16, 1949. — Right fig. Amphibious reed-swamp dominated by *Menyanthes* and *Equisetum fluviatile*. In background aquatic reed-swamps. July 19, 1949. — Photos: the writer.

the eastern one (with *Menyanthes, Equisetum fluviatile, Drepanocladus sendtneri,* and *Scorpidium* as dominants). *Menyanthes trifoliata* is the principal field-layer dominant; sociations without any bottom-layer prevail. The characteristic indicator species by which the amphibious reed-swamps differ from the *Carex elata* swamps are mostly not to be found in Möckelmossen. Both associations, and especially the amphibious reed-swamps, are represented by strongly impoverished variants in the alvar lakes, however, and no conclusions about the typical species composition can be drawn from them.

In fact, these associations, which together form the typical »lake-border swamp» of lakes with more or less eutrophic sediments and litoral soils, are rather distinct in a number of characteristic components. The amphibious reed-swamps generally are much more rich in species than the *Carex elata* swamps. Among those field-layer components which rarely or not at all proceed into the latter association are foremost to be mentioned *Calla palustris, Cicuta virosa, Comarum palustre, Corallorhiza trifida, Galium palustre* ssp. *elongatum, G. trifidum, Lastrea thelypteris, Lycopus europaeus, Peu-*

cedanum palustre, Solanum dulcamara, and the amphibious modification of *Utricularia vulgaris.* Unlike the Magnocaricion swamps, the amphibious reed-swamps are furthermore characterized by a rich and varied bottom-layer, in which may be noted *Calliergon giganteum, C. megalophyllum, Cinclidium stygium, Thuidium blandowii,* etc., not at all or only exceptionally found in the *Carex elata - Scorpidium* association.

This short description refers to the rich type of amphibious reed-swamp, found on soil rich in nutrition. Preliminarily, it may be termed the *Phragmites communis - Lastrea thelypteris - Scorpidium scorpioides* association. On account of the presence of some few exacting basibionts, *e.g. Mentha aquatica, Drepanocladus sendtneri* and *Scorpidium scorpioides,* the amphibious reed-swamp of Möckelmossen is regarded as a depauperized and unrepresentative variant of this association.

The widely distributed amphibious reed-swamps are a developmental stage of the aquatic ones, especially characteristic of eutrophic soils and sediments. They are restricted to very loose, water-drenched quagmires, and are strongly hydric plant communities — generally more hydric than the *Carex elata* swamps. After a comparatively short time, they may turn into *Carex elata* swamps, or still more frequently into more mesic plant communities, *e.g. Filipendula ulmaria* consociations. As the *Carex elata* swamps, the amphibious reed-swamps show points of resemblance with the rich fens of Du Rietz and other Swedish paludologists; they are to be considered as a special type of them. — Much attention has not been paid to the amphibious reed-swamps in the Swedish botanical literature. Almquist (1929, p. 81) has published the still best existing description.

Examples of the composition of sociations within the alvar lake variant of the *Phragmites communis - Lastrea thelypteris - Scorpidium scorpioides* association. (For explanations see pp. 89—90).

***Phragmites communis* sociation.** Alvar of Resmo, Möckelmossen, central part. July 20, 1949. — *Agrostis stolonifera* 1—2 (40), *Caltha palustris* 1 (10), *Carex fusca* 1—2 (20), *C. oederi* 1—2 (30), *Equisetum fluviatile* 1 (10), *Eriophorum latifolium* 1 (10), *Galium palustre* ssp. *eu-palustre* 1—3 (100), *Glyceria fluitans* 1 (10), *Juncus articulatus* 1—2 (50), *Lythrum salicaria* 1 (10), *Mentha aquatica* 1 (10), *M. arvensis* f. *oelandica* 1—2 (30), *Menyanthes trifoliata* 1—2 (20), *Phragmites communis* 2—4 (100), *Poa pratensis* ssp. *irrigata* 1—2 (40), *Ranunculus repens* 1—4 (50), *Scirpus palustris* 1 (10).

***Menyanthes trifoliata* sociation.** Alvar of Resmo, Möckelmossen, western shore. Transitional type to the *Scirpus palustris - Littorella* marsh. July 19, 1949. — *Agrostis stolonifera* 1—4 (60), *Alisma plantago-aquatica* 1 (10), *Equisetum fluviatile* 2—5 (100), *Mentha aquatica* 2—5 (70), *Meny-*

anthes trifoliata 3—5 (100), *Potamogeton gramineus* f. *terrestris* 1—4 (50), *Scirpus palustris* 1—2 (30). — *Bryum neodamense* 1 (10), *Scorpidium scorpioides* 1 (20). — *Chara aspera*[1] 1—5 (70).

*

It is to be noted here, that another amphibious plant community, the *Cladium mariscus* swamp, has been reported from one of the alvar lakes (Sterner 1926, p. 79, fig. 19). The writer only made a short visit to this locality and did not study the vegetation in detail. The reader is referred to Sterner's description; for a detailed study of a *Cladium* swamp in Gotland, see Ljungqvist's monograph on Mästermyr (1914, esp. pp. 49—53).

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[1] Belonging to the high-water aspect in spring. Only dead remains were found at the analysis.

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KÄRLVÄXTERNA I KROKEK.

ETT BIDRAG TILL KÄNNEDOMEN OM KOLMÅRDENS FLORA.

AV

ERIK GENBERG.

1. Kolmården. Klimatiska förhållanden och tidigare floristiska uppgifter.

Norr om Bråviken reser sig den urbergshorst, som benämnes Kolmården, vilken helt eller delvis utfyller bl. a. socknarna Kvarsebo, Krokek, Kvillinge och Simonstorp i Östergötlands län (fig. 1).

På basis av normaltemperaturen i Norrköping 1901—30 kan den ungefärliga normaltemperaturen för dessa trakter beräknas vara följande (reduktion gjord med 0,5° C på grund av höjdskillnaden):

januari	— 3,1°,
juli	+16,5°,
hela året	+ 5,7°.

På sydsluttningarna mot Bråviken äro de klimatiska förhållandena dock gynnsammare än som framgår av dessa siffror. Solstrålningen och dess reflexer mot vattenytan i förening med skyddet mot norr skapar här särskilt goda betingelser för växtlivet.

Nederbörden utgjorde vid Kolmårdssanatoriet (Krokek) i genomsnitt 1901—30.

maj	38,8 mm,	aug.	73,6 mm,
juni	60,9 mm,	hela året	548 mm.
juli	71,6 mm,		

Litteraturuppgifterna angående floran i Kolmården äro ganska sparsamma. Detta konstaterades redan av Mosén (1873), som där-

Fig. 1. Kolmården.

städes studerade mossorna (företrädesvis inom Krokeks och Kila socknar). Förefintliga äldre uppgifter över kärlväxternas utbredning hava sammanställts av KINDBERG i Östgöta Flora (sista upplagan 1901), där fyndorter i Kolmårdssocknarna finnas angivna för ett stort antal arter.

Delvis av yngre datum äro de uppgifter, som lämnats av WESTERBERG (1917), vilken under ca 30 år (1887—1917), företog floristiska undersökningar inom nordöstra Östergötland med tyngdpunkten förlagd till Risinge socken (se fig. 1). Hans undersökningar sträckte sig dock i vissa fall längre österut genom Kvillinge och fram till Krokek.

Några artförteckningar på bredare bas och av yngre datum torde icke hava publicerats men väl en och annan uppsats beträffande vissa speciella arter. Sålunda har LINDE (1912) redogjort för trenne inom Krokek förekommande växter nämligen *Rubus Bellardii, Chimaphila* och *Pleurospermum*. Om den senares växtplatser och egenart hava SYLVÉN (1912) och HORN AF RANTZIEN (1946 och 1947) publicerat utförligare uppsatser.

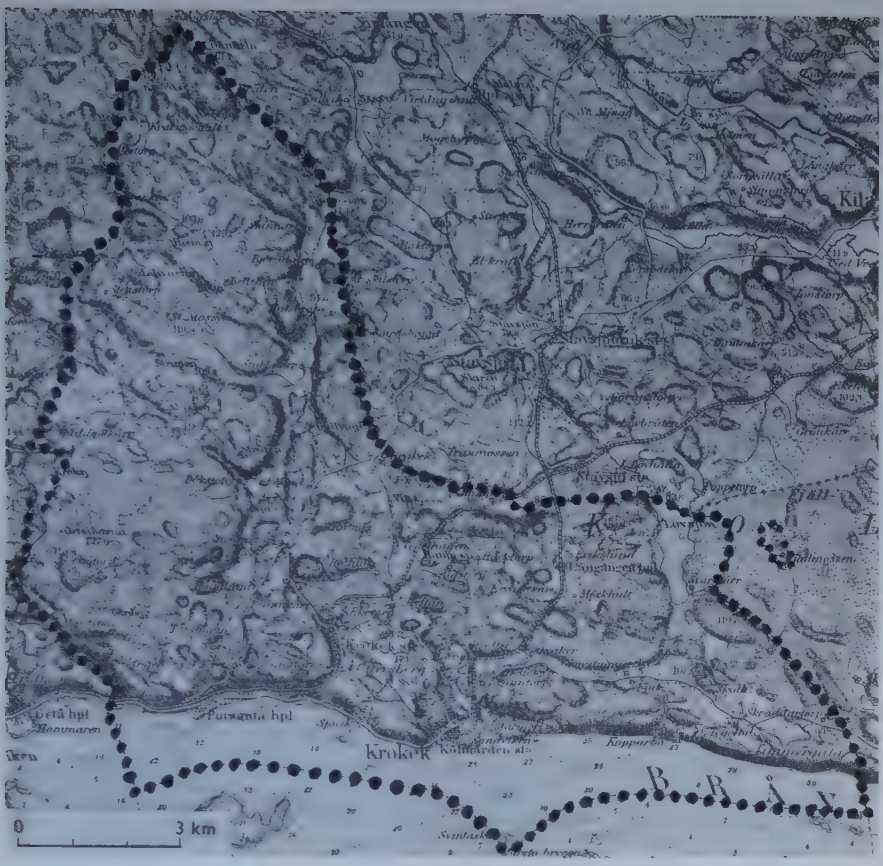

Fig. 2. Krokek sn. — För publicering godkänd i rikets allmänna kartverk den 8. nov. 1950 (D:nr Gr 654). För utförsel godkänd av försvarsstaben (K 221 Ln).

2. Krokeks socken. Geologi och topografi.

Krokeks s:n, som ligger helt på Kolmårdsmassivet, gränsar i söder till Bråviken och i norr till Kila s:n i Södermanlands län. I öster gränsar socknen till Kvarsebo och i väster till Simonstorps och Kvillinge socknar.

Utöver detta sammanhängande område omfattar socknen även en i Kvarsebo liggande mindre enklav (Fjällmossen) samt två mindre öar i Bråviken, Stenskär söder om Sjövik samt Svintaskär. Den totala arealen utgör 93 km². (Se fig. 2 samt generalstabskarta nr 56, Norrköping.)

Berggrunden utgöres liksom i Kolmården i övrigt företrädesvis av leptiter, hälleflintor, gnejs och granit. Karakteristiskt för Krokek är emellertid den i stor utsträckning i de södra delarna förefintliga förekomsten av mer eller mindre serpentinrik urkalksten. Denna till färgen grönaktiga ofiokalcit har på grund av sin vackra färg under namn av »Kolmårdsmarmor» varit föremål för brytning vid Marmorbruket i 200—300 år och senare på ett flertal olika platser i socknens södra delar. Den kalcithaltiga berggrunden förekommer huvudsakligen inom ett bälte, som sträcker sig från Sjövik i väster till Timmergata i öster och från Bråviken i söder ca 2 km mot norr. Givetvis har denna kalkhaltiga berggrund även stor betydelse för floran i dessa trakter.

Under de geologiska perioder, som följde närmast efter den sista stora nedisningen, var socknen, liksom Kolmården i övrigt, till största delen täckt av vatten. Sålunda låg i dessa trakter enl. SJÖGREN (1931):

Baltiska issjön.....	c:a	150	m	över	nuvarande havsyta
Yoldiahavet.	120—130	»	»	»	»
Ancylyssjön	c:a	75	»	»	»
Litorinahavet	»	45	»	»	»

I de högre belägna delarna utgöres jordmånen företrädesvis av grus och morän och i de uteroderade dalgångarna av sand och leror i varierande blandning. Urberget träder dock ofta i dagen, och avlagringarnas mäktighet varierar mellan 0 och flera 10-tal meter.

Socknens högsta partier ligga i väster och bilda där en platå, 100—120 m ö. h., vars högsta punkt, 155 m ö. h., ligger strax öster om Getsjötorp. Platån utgör en svårtillgänglig barrskogstrakt, som i sydväst skarpt avgränsas av Getåns ravin, vilken där utgör socknens gräns mot Kvillinge. Marken är på platåns uppskjutande partier i regel torr och hedartad, och svackorna däremellan intagas i regel av myrar. Här och där ligga mindre sjöar, av vilka den största är L. Älgsjön, och de högst belägna äro de små Getsjöarna, av vilka den högsta ligger 127 m ö. h.

Öster om denna barrskogsplatå löper från Björnsjön i norr i sydlig riktning en dalgång, som i söder vidgar sig till en odlad bygd kring Strömsfors och Svinsjön.

Ytterligare österut höjer sig terrängen åter och övergår så småningom på nytt i ett mera slutet barrskogsområde, som sträcker sig fram mot socknens östgräns mot Kvarsebo. Parallellt med Bråviks-

stranden och ca 1 km från denna löper här den skarpt markerade Oxåker-Fjuk-dalen, som längre mot öster vidgar sig i den öppnare terrängen vid Timmergata.

Alla utmed socknens väst- och nordgräns belägna småsjöar avbördas till de där angränsande socknarna med undantag för de sex Getsjöarna samt Gårdsjön, vilka avrinna genom Getån. De mera centralt belägna sjöarna bilda däremot ett för socknen internt vattensystem. Sålunda mottager Böksjön vattnet dels från L. Älgsjön och dels från Gullvagnen (genom Strålen). Böksjön i sin tur avrinner till Svinsjön, som även mottager vattnet från Vik- och Hampsjöarna. Svinsjön avrinner genom Svintunaån till Bråviken vid Sandviken. (Torsjön avrinner genom en bäck direkt till Bråviken.)

De viktigaste geografiska namnen framgå av generalstabskartan (fig. 2). Därutöver må följande lokalbeteckningar nämnas och förtydligas:

Boda = kalcithaltigt bergs- och skogsparti från »näs» i Mörtnäs ca 1 km söderut, väster järnvägen Stavsjö—Kolmården stn (den numera upprivna s. k. »Nunnebanan»). Bodaviken = stranden och ängen norr »a» i Sandviken. Brandstegen = området omkring »Te» i Tegelbr., mellan Timmergata och »Fridhem» i Kopparbo (Brandstegens utsiktsberg). Erlandstorp = höjdpartiet norr »ek» i Krokek och väster Svintunaån. Fagervik = området kring »Mar» och sydväst vägen genom »rm» i Marmorbruket. Flathällarna = strandhällar söder »et» i Marmorbruket. Frisäter = bäckravin från Bränntorp till Bråviken. Gårdsjöterrängen = området norr Gårdsjön och söder vägen Getsjötorp—Strömsfors (»Gamla Stockholmsvägen»). Gästgivaregården = området kring Krokeks ödekyrka, exkl. »Ödekyrksmossen» (se nedan). Kojtäppan = vägtriangeln kring »B» i Bränntorp och området närmast öster därom. Kopparbostigen = strandremsa och bergsstig från Flathällarna till Kopparbo. Kulla = området kring »ek stn» i Krokek stn. Marmorbruket = området öster Fagervik fram till vägen genom »u» i Marmorbruket. Munkvägen = avtagsväg från Sanatorievägen och öster järnvägskorsningen söderut mot Bråviken. Mörtnässkogen = skogspartiet nordöst Mörtnäs (öster landsvägen). Mörtnäsängen = ängsmark (huvudsakligen kärräng) söder Mörtnäs (mellan Svinsjön och landsvägen). Orrekullen = kalcithaltigt bergs- och skogsparti öster vägen Hyttan—Kolmården stn från bäcken mellan Mörtnäs och prästgården till landsvägen Krokek—Kvarsebo. Prästgården = Svinsjöns södra strand från prästgården till Svintunaån. Rödkärr = området söder Viksjön, mellan dess avlopp och järnvägen. Sandviken = stranden och samhället norr »Ko» i Kolmården stn. Stavsjömossen = mossen intill Sörmlandsgränsen, väster Lövsjön. Älgsjöavloppet = östra stranden av L. Älgsjön, sjön 500 m sydöst därom, bäcken däremellan samt terrängen omkring. Älgsjöterrängen = västra stranden av L. Älgsjön samt terrängen väster och nordväst därom

fram till sockengränsen samt nordöst därom fram till sjön söder »S» i Strupen. Ödebrotten = terrängen kring »torp» i Bränntorp från landsvägen i norr till Marmorbruket i söder och öster Kojtäppan. Ödekyrkmossen = mossen från »va» i Gullvagnen sydöst ut till Krokeks ödekyrka (vid länsgränsen).

3. Vegetationstyper.

Den skillnad i de geologiska och klimatiska förhållandena, som enligt ovan förefinnes mellan socknens nordligare (inre) och sydligare delar, inverkar starkt på sammansättningen av de olika växtsamhällena. Berggrundens kalkhalt och det varmare och mera skyddade klimatet i närheten av Bråviken ger floran därstädes en påfallande yppigare och artrikare karaktär. Detta gäller i stort sett samtliga förekommande vegetationstyper men är särskilt märkbart i lundar, å ängar och berghällar.

a. Berghällarna. Tämligen allmänna berghällsväxter i socknens nordligare delar äro *Saxifraga granulata, Silene rupestris, Spergula vernalis, Scleranthus annuus, Sedum acre, S. annuum* och *S. telephium, Carex pilulifera, Deschamsia flexuosa* samt mindre ormbunkar såsom *Polypodium* och *Woodsia*. I de södra delarna tillkomma *Geranium sanguineum* och *G. columbinum, Origanum, Satureja Acinos, Cynanchum* och *Sedum album*. På kalkhaltiga hällar dessutom *Saxifraga tridactylites* samt mera sparsamt *Geranium lucidum* och *Asplenium Ruta-muraria*. Särskilt vid Marmorbruket och Flathällarna utgör *Melica ciliata* ett karakteristiskt inslag.

b. Ängar, snår, lövängar och lundar. Liksom i övriga delar av vårt land hava de naturliga ängarna sedan länge varit utsatta för en fortgående kultivering. Där de icke lagts under plogen, utnyttjas de i allt större utsträckning som betesmarker. Smärre naturliga ängsområden — ofta i samband med lövskog — återfinnas dock här och var i Krokek.

I allmänhet representeras floran därstädes av våra allmänna ängsväxter, men understundom uppvisa dessa marker en mindre vanlig artrikedom. Oxåkerängen med sin lövängssluttning är här ännu ett vackert exempel, trots dess användning som betesmark och på senare tid även som marmorbrott. Man finner här t. ex. *Bellis, Crepis praemorsa, Serratula tinctoria, Campanula trachelium, Gentiana campestris, Origanum vulgare, Viola hirta, Vicia silvatica, Astragalus glycyphyllus, Lathyrus niger, Trifolium montanum,*

Anthyllis, Rubus aureolus, Daphne, Selinum carvifolia, Gymnadenia conopsea, Listera ovata, Platanthera bifolia, Orchis maculata och *O. sambucina, Laserpitium, Carex montana.* Där berget träder i dagen, återkomma de flesta av de ovannämnda berghällsväxterna.

Busk- och snårvegetation, som ofta förekommer, domineras av *Rosa, Rubus, Rhamnus frangula* och *Rh. cathartica, Prunus spinosa, Lonicera xylosteum* och *Viburnum opulus.* Lövträden representeras mest av björk, asp, ek, rönn, hassel och klibbal.

I de skuggigare lundarna finner man i fältskiktet vårväxter av släktena *Anemone* och *Gagea* samt *Ranunculus Ficaria* och *Pulmonaria officinalis.* Bland hasselbuskarna är *Lathraea* ej sällsynt, *Daphne* är tämligen allmän och *Corydalis pumila* förekommer här och där. Senare på sommaren komma allmänna lundgräs, *Actaea, Stachys silvatica* och *Paris.* I skogsbackarna trivas *Vicia cassubica* och *Lathyrus niger* väl tillsammans och på kalkgrund är *Epipactis atropurpurea* tämligen allmän.

c. Barrskogen. På grus- och hällmarker förekommer ofta en hedmarkstallskog med företrädesvis *Vaccinium Vitis-idaea* och — på mosanden — *Arctostaphylos* i fältskiktet. På fuktigare mark dominerar en barrblandskog med riklig *Vaccinium myrtillus*-vegetation. Tämligen allmänna inom denna vegetationstyp äro t. ex. *Pyrola chlorantha, Ramischia, Monotropa hypopitys* och *Calamagrostis arundinacea.* Den starkt försumpade barrskogen, som i regel är tallskog, är mycket allmän och bildar ofta en övergång till en utpräglad myrvegetation med inslag av *Betula pubescens.*

d. Myrar förekomma i stor omfattning. På mossarna allmänt förekommande kärlväxter äro *Drosera rotundifolia, Vaccinium oxycoccus, Andromeda polifolia, Scheuchzeria, Eriophorum vaginatum* och *Carex limosa.* Tämligen allmänna äro även *Drosera anglica* och *D. intermedia.* På den mera tuvrika marken i övergångszonen till den försumpade tallskogen finner man tämligen allmänt *Rubus chamaemorus, Vaccinium uliginosum* och *Ledum.* I ringkärren *Menyanthes, Calla, Carex rostrata, C. vesicaria, C. lasiocarpa* och *C. magellanica* samt *Eriophorum angustifolium.*

e. Sjöar. Generalstabskartan upptager ca 50 sjöar och gölar, som helt eller delvis äro belägna inom socknen. De flesta av dessa äro myrgölar, dysjöar eller andra oligotrofa vatten med *Myrica*-kantade stränder och vegetation av *Nymphaea, Nuphar, Lobelia, Isoëtes* och *Sparganium-arter.* De båda relativt stora Hamp- och Vik-

sjöarna synas vara stadda i snabb igenväxning företrädesvis genom *Phragmites, Equisetum limosum, Carex lasiocarpa* och *C. elata*. Deras avlopp domineras av *Elodea, Utricularia vulgaris* samt *Potamogeton*-arter.

f. Bråviksstranden är i Krokek ganska vegetationsfattig på grund av sin i regel branta, bergiga och steniga karaktär. Bland stenarna på stranden trivas dock *Sonchus arvensis, Valeriana officinalis, Atriplex latifolia, Angelica archangelica* och *Phalaris arundinacea* ypperligt och något längre ut i vattnet *Scirpus maritimus*. Ehuru sandstränder och strandängar nästan helt saknas, återfinnas här och där några typiska havsstrandsväxter såsom *Elymus, Glaux, Plantago maritima, Triglochin maritimum* samt *Aster tripolium*.

g. Ruderatplatser. Några utpräglade ruderatlokaler finnas icke inom socknen. Hamnområdet i Sandviken uppvisar en anmärkningsvärd fattigdom på typiska ruderatväxter. *Matricaria matricarioides, Sisymbrium officinale* och *Descurainia Sophia* kunna dock därstädes noteras och vid Fagervik *Melilotus altissimus* och *M. albus*. På järnvägsområdet vid Krokek stn finner man *Lepidium densiflorum* och *Potentilla intermedia* samt dessutom *Lithospermum arvense* och ett flertal representanter för banvallsväxterna såsom *Senecio viscosus, Chaenorrhinum minus, Alyssum Alyssoides* och *Bromus inermis*.

4. Sammanfattning av förefintliga arter.

I artlistan lämnas en sammanställning av förefintliga arter, varvid lokaluppgifter angivits, därest högst åtta växtlokaler iakttagits. I övriga fall har endast angivits allmän (a) eller tämligen allmän (ta) samt i vissa fall del av socknen, där växtlokalerna huvudsakligen äro belägna.

Lokaluppgifterna basera sig i första hand på av mig under åren 1943—46 gjorda iakttagelser, vilka 1947—50 utvidgades till en mera ingående inventering. Härvid har jag haft mycken god hjälp av bl. a. fil. dr Edvard von Krusenstjerna, Norrköping, fil. lic. Ebbe Linde, Kolmården och herr Elmer Hultgren, Timmergata, Krokek, till vilka jag därför här riktar ett hjärtligt tack för många värdefulla upplysningar.

Arter, som icke kunnat upptäckas, hava medtagits i de fall, då beläggexemplar från Krokek förefinnas i herbariet hos Riksmuseet

(S) eller i Hugo Wistrands herbarium hos Norrköpings h. allm. läroverk (W) samt eljest, om de angivits för Krokek av Kindberg (Kbg) eller Westerberg (Wbg). Motsvarande lokaluppgifter hava angivits inom parentes och hava icke kunnat verifieras. Det bör emellertid samtidigt anföras, att ett mycket stort antal funna lokaler utomordentligt väl överensstämma med uppgifterna å herbarieexemplar, som äro 40—50 år gamla.

»Artificiella» lokaler hava åstadkommits vid *Orrekullen* av kyrkoherde J. P. Linde (död 1918) och av mig vid *Erlandstorp* (tomt nr 1: 34). Desamma hava medtagits i vissa fall, då en avsevärd självspridning inträtt och angivits med asterisk.

Nomenklaturen följer Hylander utom betr. *Taraxacum*. För detta släkte liksom för *Hieracium* tillämpas Krok & Almquists nomenklatur och artuppdelning. Arter, som av Hylander angivits med *kursiv* stil (odlade och förvildade) hava ej medtagits, ej heller i regel varieteter, subspecies, former eller hybrider.

Betr. *Alchemilla*-arterna bör det anföras, att deras utbredning undersökts mindre noggrant än övriga arters, och därför är proportionsvis större än vad de anförda lokaluppgifterna giva vid handen.

På grund av den egendomliga utbredning, som karakteriserar *Pleurospermum*, skola dess växtlokaler något närmare angivas än som varit lämpligt i artlistan.

Vid Erlandstorp funnos 1950 tvenne blommande exemplar härrörande antingen från av mig 1941 insått frö eller från självsådd av ett inplanterat exemplar, som blommade 1945.

Marmorbruket. Tvenne bestånd på ca 100 m avstånd finnas vid »ru» i Marmorbruket på vägens södra sida. Det västra bestod 1950 av ett 30-tal blommande exemplar och det östra av ett 60-tal.

Orrekullen. Här finnas egentligen tvenne lokaler. Den ena inplanterad av Linde vid stugorna omedelbart sydöst transformatorn vid prästgården. Ett flertal blommande exemplar 1950. Den andra lokalen möjligen spontan på nordsluttningen mot stugan »Skymundan». Tre blommande exemplar 1950.

Oxåker. 100-tals blommande exemplar på både sidor om landsvägen Krokek—Kvarsebo, öster om avtagsvägen till Oxåker.

Brandstegen. I barrskog med inslag av asp, alldeles intill stigen, som från Timmergata leder till utsiktsberget och nära detta. Fyra blommande exemplar och talrika bladrosetter 1950.

Raggan. Tvenne lokaler finnas. Den ena vid första »g» i Raggan, alldeles vid länsgränsen, ca 150 m söder om vägen till Krokeks ödekyrka. Ett 80-tal blommande exemplar 1950. Den andra på ömse sidor om järnvägen (företrädesvis *söder* om denna) söder »ag» i Raggan. Ett 50-tal blommande exemplar.

Fjällmossen. Ett blommande exemplar och talrika bladrosetter i en lövskogsdunge öster om vägen, som leder från gårdarna i nordlig riktning mot mossen.

Summan av de i artlistan upptagna arterna utgör:

Funna 1947—50	727
Äldre beläggexemplar i herbarier (S och W)	32
Angivna av auktor (Kbg och Wbg)	11
Totalt	770

Vid jämförelse med de sammanställningar över de olika arternas utbredning, som uppgjorts av HULTÉN (1950), finner man, att några för socknen oväntade arter knappast kunnat konstateras, men att ytterligare ett mycket stort antal därstädes borde kunna återfinnas, och ytterligare efterforskningar komma naturligtvis att vidga såväl art- som lokalförteckning.

Nya nordöstliga utposter hava dock konstaterats för *Quercus petraea* och *Scirpus multicaulis*. Vidare hava nordöstliga utposter verifierats för *Arnica montana, Cirsium acaule, Hypochaeris radicata, Leontodon hispidus, Pedicularis silvatica* samt *Rubus Bellardii*.

Artlista.

Acer platanoides. ta. — *Achillea millefolium*. a. — *A. ptarmica*. ta. — *Acorus calamus*. Svinsjön vid Prästgården, Uttersberg, Kulla och Mörtnäs. —*Actaea spicata*. ta. — *Adoxa moschatellina*. Prästgården. — *Aegopodium podagraria*. ta. — *Aethusa cynapium*. ta. — *Agropyron caninum*. Prästgården, Kulla, Bränntorp, Frisäter, Holmtorp, Marmorbruket, Kopparbostigen, Timmergata. — *A. repens*. a. — *Agrimonia eupatoria*. a. — *Agrostemma Githago*. W. (Sandviken). — *Agrostis canina*. a. — *A. stolonifera*. a. — *A. tenuis*. a. — *Ajuga pyramidalis*. a. — *Alchemilla acutiloba*. S. (Sandviken, Gruvstugan, Timmergata). — *A. filicaulis*. Erlandstorp, Timmergata, Bränntorp. — *A. glabra*. ta. — *A. glaucescens*. ta. — *A. pastoralis*. Erlandstorp, Fagervik, Bränntorp. — *A. subcrenata*. Serveringsberget, Fagervik, Timmergata, Torp, Gusäter, Mörtnässkogen, Vik. — *A. subglobosa*. Boda. — *A. vestita*. Erlandstorp, Serveringsberget, Oxåker. — *Alisma Plantago-aquatica*. a. — *Alliaria officinalis*. Erlandstorp, Sandviken. — *Allium oleraceum*. a. — *A. schoenoprasum*. Serveringsberget, Fagervik, Marmorbruket. — *A. vineale*. Sandviken — *Alnus glutinosa*. a. — *Alopecurus aequalis*. Sanatoriet, Munkvägen, Uttersberg, Orrekullen, Mörtnässkogen. — *A. geniculatus*. a. — *A. pratensis*. a. — *Alyssum Alyssoides*. Krokek stn. — *Anagallis arvensis*. S. — *Anchusa arvensis*. ta. — *A. officinalis*. ta. — *Andromeda polifolia*. ta. — *Anemone hepatica*. a. — *A. nemorosa*. a. — *Angelica archangelica*. a. vid Bråviksstranden. — *A. silvestris*.

a. — *Antennaria dioeca.* a. — *Anthemis arvensis.* Erlandstorp, Fagervik, Kopparbo, Rotnäs, Gusäter. — *A. cotula.* Kbg. (Marmorbruket). — *A. tinctoria.* ta. — *Anthoxanthum odoratum.* a. — *Anthriscus silvestris.* a. — *Anthyllis vulneraria.* ta. — *Apera spica venti.* S. (Vik). — *Aquilegia vulgaris.* ta. — *Arabidopsis Thaliana.* a. — *Arabis hirsuta.* ta. — *Arctium Lappa.* Frisäter. — *A. minus.* ta. — *A. tomentosum.* ta. — *Arctostaphylos Uva-ursi.* a. — *Arenaria serpyllifolia.* a. — *Armeria maritima.* Svinstaskär, Porsgata, Erlandstorp, Sandviken, Bodaviken, Gästgivargården. — *Arnica montana.* Getsjötorp, Torstugan, Långängen hpl. — *Artemisia absinthium.* ta. — *A. campestris.* ta. nära Bråviken. — *A. vulgaris.* a. — *Asparagus officinalis.* Getå och Flathällarna vid Bråviksstranden. — *Asperugo procumbens.* Sandviken, Marmorbruket. — *Asperula tinctoria.* Oxåker vid Uppgården. — *Asplenium Ruta-muraria.* Serveringsberget, Marmorbruket, Orrekullen. — *A. septentrionale.* ta. — *A. trichomanes.* a. — *Aster tripolium.* Stenskär, Svinstaskär, Porsgata, Serveringsberget, Bodaviken, Flathällarna, Kopparbostigen, Tinmergata. — *Astragalus glycyphyllus.* ta. — *Athyrium filix femina.* a. — *Atriplex latifolia.* a. vid Bråviksstranden. — *A. longipes.* Stenskär, Svinstaskär, Getå. — *A. patula.* ta. — *Avena elatior.* ta. — *A. pratensis.* a. — *A. pubescens.* a.

Barbarea stricta. Svinstaskär, Getå, Sandviken, Frisäter, Bränntorp, Kulla, Orrekullen. — *B. vulgaris.* a. — *Bellis perennis.* Prästgården, Oxåker, Timmergata, Hacktorp. — *Berberis vulgaris.* ta. — *Berteroa incana.* Porsgata, Erlandstorp, Sandviken. — *Betula pubescens.* a. — *B. verrucosa.* a. — *Bidens cernua.* Tegelhagen, Vik. — *B. tripartita.* a. — *Botrychium lunaria.* Orrekullen. — *Brachypodium pinnatum.* Kopparbostigen. — *B. silvaticum.* Marmorbruket (E. von Krusenstjerna). — *Brassica campestris.* Stenstorp, Svartkärr. — *B. nigra.* S. — *Briza media.* a. — *Bromus arvensis.* Erlandstorp, Sandviken. — *B. erectus.* Kbg. (Marmorbruket). — *B. hordeaceus.* a. — *B. inermis.* Getå, Sandviken, Marmorbruket, Kopparbo, Krokek stn, Orrekullen, Tegelhagen, Älgstorp. — *B. secalinus.* S. (Orrekullen). — *B. sterilis.* S. (Uttersberg, Timmergata), W. (Sandviken). — *B. tectorum.* Getå, Sandviken, Krokek stn. — *Bunias orientalis.* Porsgata, Marmorbruket, Krokek stn, Älgstorp.

Calamagrostis arundinacea. a. — *C. canescens.* a. — *C. epigeios.* ta. — *C. neglecta.* Mörtnäs, Böksjötorp. — *Calla palustris.* a. — *Callitriche hamulata.* Oxåker, Mörkhult. — *C. hermaphroditica.* Timmergata. — *C. polymorpha.* Orrekullen, Boda, Timmergata, Tegelhagen. — *C. verna.* a. — *Calluna vulgaris.* a. — *Calystegia sepium.* Erlandstorp, Sandviken, Flathällarna, Kopparbostigen, Boda, Mörtnässkogen, Eketorp. — *Caltha palustris.* a. — *Camelina Alyssum.* W. (Raggan). — *C. microcarpa.* Sandviken, Kojtäppan. — *Campanula cervicaria.* Timmergata, Stenstorp, Björndalen, Skinnarbo. — *C. latifolia.* Frisäter. — *C. patula.* Erlandstorp (tillf.), Betlehem (tillf.), Hyttan (ymnigt). — *Campanula persicifolia.* a. — *C. rapunculoides.* ta. — *C. rotundifolia.* a. — *C. trachelium.* Fagervik, Marmorbruket, Kopparbo, Mörtnässkogen, Oxåker. — *Capsella bursa pastoris.* a. — *Cardamine amara.* Munkvägen, Holmtorp. — *C. hirsuta.* Erlandstorp, Kopparbo. — *C. pratensis.* a. — *Cardaminopsis arenosa.* Krokek stn. — *Carduus crispus.* Bodaviken, Frisäter, Fagervik,

Uttersberg, Prästgården, Mörtnäs. — *Carex acuta.* ta. — *C. acutiformis.* Rödkärr. — *C. caespitosa.* ta. — *C. canescens.* a. — *C. capillaris.* Kbg. (Fagervik). — *C. caryophyllea.* ta. — *C. chordorrhiza.* Gäddgölkärr. — *C. contigua.* ta. — *C. diandra.* Fagervik, Mörtnäsängen, Gullvagnen, Rotnäs, Rödkärr, Ödekyrkmossen, Vik. — *C. digitata.* a. — *C. dioeca.* ta. — *C. disticha.* ta. — *C. divulsa.* S. (Orrekulla). — *C. echinata.* a. — *C. elata.* ta. — *C. elongata.* Sandviken, Bränntorp, Uttersberg. — *C. ericetorum.* ta. — *C. flacca.* ta. — *C. flava.* ta. — *Carex fusca.* a. — *C. globularis.* Gårdsjöterrängen. — *C. hirta.* ta. — *C. Hostiana.* Skinnarbo. — *C. lasiocarpa.* a. — *C. leporina.* a. — *C. limosa.* a. — *C. magellanica.* ta. — *C. montana.* Uttersberg, Prästgården, Mörtnässkogen, Boda, Gusäter, Kojtäppan, Holmtorp, Oxåker. — *C. Oederi.* ta. — *C. pallescens.* a. — *C. panicea.* a. — *C. pauciflora.* ta. — *C. pilulifera.* a. — *C. Pseudocyperus.* Sjövik, Vik. — *C. pulicaris.* Tegelhagen, Raggan. — *C. remota.* Kopparbostigen, Stenstorp. — *C. rostrata.* a. — *C. vaginata.* Gårdsjöterrängen, Strupen. — *C. vesicaria.* a. — *Carlina vulgaris.* ta. (ssp. *longifolia* vid Marmorbruket). — *Carum carvi.* ta. — *Centaurea Cyanus.* ta. — *C. jacea.* a. — *C. scabiosa.* Frisäter, Fagervik. — *Cerastium aquaticum.* Kbg. (Getå). — *C. arvense.* Erlandstorp, Fagervik, Oxåker, Svartkärr. — *C. brachypetalum.* Kopparbostigen. Kbg. (Marmorbruket). — *C. glomeratum.* S. (Prästgården). — *C. glutinosum.* W. (Flathällarna). — *C. holostoides.* a. — *Cerastium semidecandrum.* ta. — *Ceratophyllum demersum.* Svinsjön (vid dess utlopp). — *Chaenorrhinum minus* Getå, Krokek stn. — *Chamenerion angustifolium.* a. — *Chelidonium majus.* a. — *Chenopodium album.* a. — *C. Bonus-Henricus.* Bodaviken, Fagervik, Marmorbruket, Kopparbo, Timmergata, Uttersberg, Älgstorp, Skräddartorp. — *C. glaucum.* Uttersberg. — *C. polyspermum.* W. (Marmorbruket). — *Chimaphila umbellata.* Porsgata, Frisäter, Brandstegen. — *Chrysanthemum leucanthemum.* a. — *C. vulgare.* a. — *Chrysosplenium alternifolium.* ta. — *Cichorium intybus.* Erlandstorp (tillf.), Sandviken (tillf.), Eketorp. — *Cicuta virosa.* Porsgata, Rotnäs, Ödekyrkmossen. — *Circaea alpina.* Munkvägen, Erlandstorp. — *Cirsium acaule.* Bodaviken, Oxåker. — *C. arvense.* a. — *C. heterophyllum.* Kopparbostigen, Holmtorp, Oxåker, Eketorp, Stubbetorp, Björndalen. — *C. palustre.* a. — *C. vulgare.* a. — *Conium maculatum.* Kbg. (Orrekulla). — *Convallaria majalis.* a. — *Convolvulus arvensis.* ta. — *Corallhorrhiza trifida.* Fjuk, Älgstorp, Raggan, Stavsjömossen. — *Corydalis pumila.* Serveringsberget, Fagervik, Kopparbostigen. — *Corylus avellana.* a. — *Cotoneaster integerrimus.* ta. inom kalcitområdet. — *Crataegus calycina.* ta. — *C. monogyna.* Fagervik, Kojtäppan, Brandstegen, Timmergata. — *Crepis capillaris.* Marmorbruket. — *C. paludosa.* Holmtorp, Eketorp. — *C. praemorsa.* ta. — *C. tectorum.* ta. — *Cynanchum vincetoxicum.* ta. — *Cynoglossum officinale.* ta. — *Cynosurus cristatus.* ta. — *Cystopteris fragilis.* a.

Dactylis glomerata. a. — *Daphne mezereum.* ta. — *Daucus carota.* Fagervik. — *Delphinium consolida.* Kulla. — *Deschampsia bottnica.* Kbg. (Marmorbruket). — *D. caespitosa.* a. — *D. flexuosa.* a. — *Descurainia Sophia.* Sjövik, Erlandstorp, Sandviken, Fagervik, Nöden, Gästgivargården. — *Dianthus deltoides.* ta. — *Digitalis purpurea.* Munkvägen, Kop-

parbo, Algutsbo, Eketorp. (Sann. förv. å samtl. lokaler.) — *Draba muralis.* Orrekullen. — *Drosera anglica.* ta. — *D. intermedia.* ta. — *D. rotundifolia.* a. — *Dryopteris austriaca.* a. — *D. filix mas.* a.

Echium vulgare. Fagervik, Kopparbo, Algutsbo. — *Elodea canadensis.* Avloppen från Vik- och Hampsjöarna t. ex. vid Rödkärr och Älgstorp. — *Elymus arenarius.* Stenskär, Svinstaskär, Sjövik, Sandviken, Frisäter, Fagervik. — *Empetrum nigrum.* a. — *Epilobium adenocaulon.* Frisäter, Orrekullen. — *E. collinum.* Fagervik, Kopparbostigen. — *E. montanum.* a. — *E. obscurum.* Porsgata. S. (Timmergata, Kopparbo). — *E. palustre.* a. — *E. parviflorum.* Frisäter, Fagervik, Mörtnäsängen, Bränntorp, Holmtorp. — *E. roseum.* Frisäter, Marmorbruket. — *E. rubescens.* ta. — *E. tetragonum.* Kbg. (Torskär). — *Epipactis atropurpurea.* ta. inom kalcitområdet. T. ex. Erlandstorp, Serveringsberget, Fagervik, Marmorbruket, Bränntorp, Kojtäppan, Ödebrotten, Oxåker, Orrekullen, Boda, Gusäter, Ervastekärr. — *E. Helleborine.* Gusäter. — *E. palustris.* S. (Orrekullen). — *Epipogum aphyllum.* Kbg. (Marmorbruket). — *Equisetum arvense.* a. — *E. fluviatile.* a. — *E. hiemale.* ta. — *E. palustre.* ta. — *E. pratense.* ta. — *E. silvaticum.* a. — *Erigeron acre.* a. — *E. canadense.* Getå, Porsgata, Krokek stn, Eketorp, Raggan. — *Eriophorum angustifolium.* a. — *E. gracile.* Kranken. — *E. latifolium.* Stavsjömossen. — *E. vaginatum.* a. — *Erodium cicutarium.* a. — *Erophila verna.* a. — *Erysimum cheiranthoides.* a. — *E. hieracifolium.* Svinstaskär, Fagervik, Marmorbruket. — *Eupatorium cannabinum.* Marmorbruket, Flathällarna, Kopparbostigen. — *Euphorbia cyparissias.* Erlandstorp, Sandviken, Torp, Gäddgölkärr. — *E. Esula.* Sandviken. — *E. helioscopia.* a. — *E. peplus.* Sandviken, Marmorbruket. — *Euphrasia brevipila.* a. — *E. curta.* Timmergata. — *E. micrantha.* S. (Rotnäs).

Festuca arundinacea. ta. vid Bråviken. — *F. ovina.* a. — *F. pratensis.* a. — *F. rubra.* a. — *Filago arvensis.* a. — *Filipendula ulmaria.* a. — *F. vulgaris.* ta. — *Fragaria moschata.* Porsgata, Kopparbo. — *F. vesca.* a. — *F. viridis.* Erlandstorp, Sandviken, Serveringsberget, Fagervik, Flathällarna, Prästgården, Orrekullen, Oxåker. — *Fraxinus excelsior.* ta. — *Fumaria officinalis.* a.

Gagea lutea. a. — *G. minima.* a. — *Galeopsis bifida.* a. — *G. speciosa.* a. — *G. tetrahit.* a. — *Galium aparine.* ta. — *G. boreale.* a. — *G. mollugo.* ta. — *Galium palustre.* a. — *G. trifidum.* Älgstorp. — *G. uliginosum.* a. — *G. Vaillantii.* a. — *G. verum.* a. — *Genista tinctoria.* Porsgata (sann. förv.). — *Gentianella campestris.* Uttersberg, Oxåker, Rotnäs, Skinnarbo. — *Geranium bohemicum.* Kopparbostigen, Timmergata, Oxåker, Svartkärr. — *G. columbinum.* ta. inom kalcitområdet. — *G. lucidum.* Prästgården, Orrekullen, Boda, Gusäter, Kopparbo. — *G. pratense.* W. (Marmorbruket). — *G. pusillum.* a. — *G. robertianum.* a. — *G. sanguineum.* ta. — *G. silvaticum.* a. — *Geum rivale.* a. — *G. urbanum.* a. — *Glaux maritima.* Stenskär, Svinstaskär, Porsgata, Serveringsberget, Bodaviken. — *Glechoma hederacea.* a. — *Glyceria fluitans.* a. — *G. maxima.* Porsgata, Frisäter, Timmergata. — *Gnaphalium silvaticum.* a. — *G. uliginosum.* a. — *Goodyera repens.* ta. — *Gymnadenia conopsea.* Oxåker, Kvarnsjöhult.

Hammarbya paludosa. Torstugan, Svartkärr, Älgsjöterrängen, Raggan,

Stavsjömossen, Kranken. — *Hedera helix.* Kojtäppan, Kopparbo. Båda lokalerna säkert spontana. — *Helianthemum nummularium.* ta. — *Heracleum Sphondylium.* ta. — *Herminium monorchis.* Kbg. (Marmorbruket). — *Herniaria glabra.* ta. — *Hieracium aurantiacum.* Erlandstorp, Sandviken. — *H. auricula.* a. — *H. dubium.* a. — *H. murorum.* a. — *H. pilosella.* a. — *H. rigidum.* a. — *H. silvaticum.* a. — *H. umbellatum.* a. — *Hippuris vulgaris.* Fagervik, Timmergata, Mörtnäs, Rotnäs, Rödkärr, Böksjötorp. — *Holcus lanatus.* Erlandstorp, Krokek stn. — *Humulus lupulus.* Oxåker, Tegelhagen, Kvarnsjöhult. — *Hydrocharis morsus ranae.* Fagervik. — *Hyoscyamus niger.* Erlandstorp, Fagervik, Marmorbruket, Tegelhagen. — *Hypericum maculatum.* a. — *H. montanum.* Getå, Porsgata, Kopparbostigen, Orrekullen, Boda, Gusäter, Mörtnässkogen. — *H. perforatum.* a. — *Hypochaeris maculata.* ta. — *H. radicata.* Gullvagnens badställe, Strömsfors.

Impatiens Noli-tangere. Munkvägen. — *Inula salicina.* Marmorbruket, Kopparbostigen, Orrekullen. — *Iris pseudacorus.* Svinstaskär, Porsgata, Mörtnäs, Algutsbo, Torp, Strömsfors, Svartkärr, Raggan. — *Isoëtes echinosporum.* Getsjön p. 127, Gäddgölkärr, Älgsjöterrängen, Älgsjöavloppet, Böksjön, Nöden. — *I. lacustre.* Gårdsjön, Gullvagnen, Skrålen.

Jasione montana. Sjövik, Kopparbostigen, Brandstegen. — *Juncus alpinus.* Timmergata, Raggan. — *Juncus articulatus.* a. — *J. bufonius.* a. — *J. bulbosus.* a. — *J. compressus.* Fagervik, Timmergata, Uttersberg, Boda, Bränntorp, Oxåker. — *J. conglomeratus.* a. — *J. effusus.* a. — *J. filiformis.* ta. — *J. Gerardi.* a. vid Bråviken. — *J. macer.* Getå vid Stordalen, Vik. — *Juniperus communis.* a.

Knautia arvensis. a.

Lactuca muralis. ta. — *Lamium album.* Frisäter. — *L. amplexicaule.* ta. — *L. hybridum.* Erlandstorp, Boda, Strömsfors. — *L. molluccellifolium.* S. (Uttersberg). — *L. purpureum.* a. — *Lappula Myosotis.* Marmorbruket. — *Lapsana communis.* a. — *Laserpitium latifolium.* ta. — *Lathraea squamaria.* Marmorbruket, Kopparbostigen, Timmergata, Prästgården, Eketorp, Tegelhagen. — *Lathyrus heterophyllus.* Kbg. (Björndalen). — *L. montanus.* a. — *L. niger.* ta. — *L. palustre.* Uttersberg, Mörtnäsängen. — *L. pratensis.* a. — *L. silvestre.* ta. — *L. vernus.* Kopparbo, Timmergata, Brandstegen, Prästgården, Orrekullen, Holmtorp, Oxåker. — *Ledum palustre.* a. — *Lemna minor.* a. — *L. trisulca.* Fagervik. — *Leontodon autumnalis.* a. — *L. hispidus.* Sandviken, Bodaviken, Frisäter, Boda. — *Leonurus cardiaca.* Erlandstorp, Marmorbruket, Kojtäppan, Tegelhagen. — *Lepidium campestre.* Timmergata. — *L. densiflorum.* Krokek stn. — *L. ruderale.* Erlandstorp, Sandviken. — *Ligustrum vulgare.* Kopparbo (sann. förv.). — *Linaria vulgaris.* ta. — *Linnea borealis.* ta. — *Linum catharticum.* ta. — *Listera cordata.* Fjuk, Gårdsjöterrängen, Älgsjöterrängen, Ödekyrkmossen, Stavsjömossen. — *L. ovata.* Fagervik, Kojtäppan, Oxåker. — *Lithospermum arvense.* Krokek stn. — *L. officinale.* S. (Kopparbo). — *Lobelia Dortmanna.* ta. — *Lolium perenne.* Erlandstorp, Ödebrotten, Marmorbruket, Kopparbo. — *Lonicera periclymenum.* Timmergata. — *L. xylosteum.* ta. — *Lotus corniculatus.* a. — *Luzula campestris.* a. — *L. luzuloides.* Getå. — *L. multiflora.* a. — *L. pallescens.* Algutsbo (E. von

Krusenstjerna), Marmorbruket. — *L. pilosa.* a. — *Lychnis flos cuculi.* a. — *Lycopodium annotinum.* a. — *L. clavatum.* a. — *L. selago.* Ödebrotten, Kopparbo, Mörkhult, Svartkärr, Vik, Stavsjömossen, Skinnarbo. — *Lycopus europaeus.* ta. — *Lysimachia nummularia.* Algutsbo, Boda. — *L. thyrsiflora.* ta. — *L. vulgaris.* a. — *Lythrum salicaria.* a.

Majanthemum bifolium. a. — *Malus silvestris.* ta. — *Malva alcea.* Mörkhult. — *M. Moschata.* ta. — *M. neglecta.* Erlandstorp, Sandviken, Fagervik, Marmorbruket, Dragtorpet, Uttersberg, Gästgivargården. — *M. pusilla.* S. (Orrekulla). — *Matricaria chamomilla.* ta. — *M. maritima.* a. — *M. matricarioides.* a. — *Matteuccia Struthiopteris.* Getå, Kulla, Eketorp, Hyttan. — *Medicago falcata.* Sandviken. — *M. lupulina.* a. — *Melampyrum arvense.* W. (Frisäter). — *M. cristatum.* Prästgården, Oxåker, Kopparbostigen. — *M. nemorosum.* Erlandstorp.* — *M. pratense.* a. — *M. silvaticum.* a. —*Melandrium album.* Getå, Erlandstorp, Sandviken, Fagervik, Marmorbruket, Gusäter. — *M. noctiflorum.* W. (Sandviken). — *Melica ciliata.* Serveringsberget, Marmorbruket, Flathällarna, Kopparbostigen, Timmergata. — *M. nutans.* a. — *Melilotus albus.* Fagervik, Marmorbruket. — *M. altissimus.* Fagervik, Marmorbruket. — *Mentha aquatica.* Porsgata. — *M. arvensis.* a. — *Menyanthes trifoliata.* a. — *Milium effusum.* Getå. — *Moehringia trinervia.* a. — *Molinia caerulea.* a. — *Moneses uniflora.* Erlandstorp, Serveringsberget, Kopparbo, Boda, Långängen, Rödkärr. — *Monotropa hypophegea.* Orrekullen. — *M. hypopitus.* ta. — *Montia lamprosperma.* S. (Råsätersbackarna). — *Myosotis arvensis.* a. — *M. discolor.* Tegelhagen. — *M. hispida.* ta. — *M. laxa.* ta. — *M. palustris.* a. — *M. silvatica.* Frisäter, Fagervik, Prästgården. — *M. stricta.* a. — *Myosurus minimus.* Erlandstorp, Uttersberg, Ervastekärr, Mörkhult. — *Myrica gale.* a. — *Myriophyllum alterniflorum.* Torp. W. (Viksjön). — *M. spicatum.* Bråviken vid Sandviken och Fagervik, Torsjön, Strömsfors, Nöden. — *M. verticillatum.* Svinsjön och Svintunaån. — *Myrrhis odorata.* Marmorbruket.

Nardus stricta. a. — *Neottia Nidus-avis.* Brandstegen. — *Nepeta cataria.* Erlandstorp. — *Nuphar luteum.* a. — *Nymphaea alba.* a.

Odontites ruber. Bränntorp, Timmergata, Strömsfors, Rödkärr. — *Oenanthe aquatica.* Erlandstorp, Bränntorp, Kulla. — *Oenothera biennis.* Getå, Eketorp, Algutsbo, Strömsfors. — *Ononis hircina.* Boda. — *Orchis maculata.* ta. — *O. sambucina.* Oxåker, Kopparbostigen, Mörtnässkogen. — *O. strictifolia.* S. (Kärräng 700 m öster Sandviken). — *O. Traunsteineri.* Fjällmossen (möjligen i Kvarsebo sn.). — *Origanum vulgare.* ta. — *Oxalis acetosella.* a.

Papaver dubium. ta. — *Paris quadrifolia.* ta. — *Parnassia palustris.* ta. — *Pastinaca sativa.* Marmorbruket, Timmergata. — *Pedicularis palustris.* ta. — *P. silvatica.* Böksjötorp, Älgstorp, Hacktorp, Skinnarbo. — *Peplis Portula.* S. (Munkslätten, Marmorbruket). — *Petasites hybridus.* Orrekullen.* — *Peucedanum palustre.* a. — *Phalaris arundinacea.* a. — *Phleum phleoides.* Erlandstorp, Frisäter, Fagervik, Marmorbruket, Krokek stn, Ödebrotten, Gusäter. — *P. pratensis.* a. — *Phragmites communis.* a. — *Picea Abies.* a. — *Pimpinella major.* S. (Marmorbruket). — *P. saxifraga.* a. — *Pinguicula vulgaris.* Holmtorp, Tegelhagen, Hacktorp. — *Pinus sil-*

vestris. a. — *Plantago lanceolata*. a. — *P. major*. a. — *P. maritima*. Stenskär, Svinstaskär, Getå, Porsgata, Serveringsberget, Bodaviken, Kopparbostigen, Timmergata. — *P. media*. a. — *Platanthera bifolia*. ta. — *P. chlorantha*. S. (Orrekullen). — *Pleurospermum austriacum*. Erlandstorp*, Marmorbruket, Orrekullen, Oxåker, Brandstegen, Raggan, Fjällmossen. — *Poa annua*. a. — *P. compressa*. ta. — *P. nemoralis*. a. — *P. palustris*. Erlandstorp, Ödebrotten, Mörtnäs. — *P. pratensis*. a. — *P. trivialis*. a. — *Polemonium coeruleum*. Sandviken (sann. förv.). — *Polygala vulgaris*. a. — *Polygonatum multiflorum*. Getå, Orrekullen. — *P. odoratum*. a. — *Polygonum amphibium*. Strömsfors. (E. von Krusenstjerna). — *P. aviculare*. a. — *P. convolvulus*. a. — *P. dumetorum*. Svinstaskär, Sandviken, Fagervik, Marmorbruket, Kopparbostigen, Munkvägen, Eketorp. — *P. hydropiper*. a. — *P. lapathifolium*. a. — *P. minus*. Sandviken. — *P. nodosum*. Mörtnäs, Tegelhagen, Rotnäs, Rödkärr. — *P. oxyspermum*. W. (Marmorbruket). — *P. persicaria*. Dragtorpet, Boda, Ervastekärr, Älgsjöavloppet. — *P. viviparum*. ta. — *Polypodium vulgare*. a. — *Populus tremula*. a. — *Potamogeton alpinum*. Tegelhagen, Rödkärr, Raggan. — *P. crispum*. Bråviken vid Sandviken och Kopparbostigen (lösryckta exemplar efter storm). — *P. gramineus*. Timmergata. — *P. natans*. a. — *Potamogeton oblongus*. Gårdsjön, Brännkärr, Gäddgölkärr, Älgsjöavloppet. — *P. obtusifolium*. Uttersberg, Rödkärr, Vik. — *P. pectinatum*, ta. i Bråviken. — *P. perfoliatum*. ta. i Bråviken, Svintunaån. *P. pusillum*. Timmergata, Rödkärr, Raggan, Fjällmossen. — *Potentilla anserina*. a. — *P. argentea*. a. — *P. Crantzii*. Mörtnässkogen, Fjällmossen. — *P. erecta*. a. — *P. intermedia*. Krokek stn. — *P. norvegica*. Strömsfors, Gäddgölkärr. — *P. palustris*. a. — *P. reptans*. a. — *P. Tabernaemontani*. ta. — *Primula farinosa*. Holmtorp. — *P. veris*. a. — *Prunella vulgaris*. a. — *Prunus avium*. ta. — *P. padus*. ta. — *P. spinosa*. a. — *Pteridium aquilinum*. a. — *Pulmonaria officinalis*. ta. — *Pyrola chlorantha*. ta. — *P. media*. Stavsjömossen. — *P. minor*. a. — *P. rotundifolia*. ta.

Quercus petraea. Getå (mellan landsvägen och järnvägen, intill sockengränsen). — *Q. robur*. a.

Ramischia secunda. a. — *Ranunculus acris*. a. — *R. auricomus*. a. — *R. bulbosus*. ta. — *R. ficaria*. ta. — *R. Flammula*. ta. — *R. lingua*. Prästgården, Älgstorp. — *R. obtusiflorus*. a. i Bråviken. — *R. polyanthemus*. ta. — *R. repens*. a. — *R. sceleratus*. ta. — *R. trichophyllus*. Mörtnäsängen, Bränntorp, Strömsfors. — *Raphanus raphanistrum*. ta. — *Rhamnus catharticus*. ta. — *R. frangula*. ta. — *Rhinanthus minor*. a. — *Rhynchospora alba*. ta. — *R. fusca*. Gårdsjön, Kranken. — *Ribes alpinum*. ta. — *R. nigrum*. Erlandstorp, Sandviken, Frisäter, Kopparbo, Munkvägen, Uttersberg, Mörtnäs, Gästgivargården. — *R. silvestre*. Munkvägen, Orrekullen, Kulla, Eketorp. — *R. Uva-crispa*. ta. — *Rorippa islandica*. Frisäter, Holmtorp, Mörtnäs, Kulla, Strömsfors, Tegelhagen. — *R. silvestris*. W. (Bränntorp). — *Rosa canina*. a. — *R. dumalis*. Fagervik, Kopparbostigen, Eketorp, Gästgivargården. — *R. majalis*. Fagervik, Kopparbostigen, Kopparbo, Kojtäppan, Prästgården. — *R. rubiginosa*. Mörtnäs. — *R. tomentosa*. Orrekullen, Oxåker. — *R. villosa*. a. — *Rubus aureolus*. ta. — *R. Bellardii*. Kopparbostigen, Kopparbo, Brandstegen, Timmergata. Mångenstädes mellan

Kopparbo och Timmergata. — *R. caesius.* Fagervik, Marmorbruket, Kopparbostigen, Kopparbo, Timmergata. — *R. chamaemorus.* a. — *R. horridus.* Orrekullen.* — *R. idaeus.* a. — *R. nessensis.* ta. — *R. saxatilis.* a. — *R. thyrsanthus.* Kopparbostigen, Kopparbo, Timmergata. — *R. Wahlbergii.* Kopparbo. S. (Timmergata). — *Rumex acetosa.* a. — *R. acetosella.* a. — *R. crispus.* a. — *R. domesticus.* a. — *R. hydrolapathum.* Porsgata, Fagervik. — *R. obtusifolius.* ta. — *R. maritimus.* Frisäter.

Sagina procumbens. a. — *Salix aurita.* a. — *S. caprea.* a. — *S. cinerea.* ta. — *S. depressa.* Uttersberg. Kbg (Marmorbruket). — *S. fragilis.* Getå, Erlandstorp, Frisäter, Fjuk, Eketorp. — *S. hastata.* S. (Mellan Kulla och Uttersberg). — *S. pentandra.* ta. — *S. phylicifolia.* ta. — *S. repens.* a. — *Sambucus nigra.* Prästgården, Gäddgölkärr. — *S. racemosa.* Porsgata, Frisäter, Munkvägen, Orrekullen, Kulla, Eketorp. — *Sanicula europaea.* Serveringsberget, Kopparbostigen, Kopparbo, Kojtäppan, Oxåker. —*Sanguisorba minor.* Porsgata. — *Sarothamnus scoparia.* Timmergata. — *Satureja Acinos.* ta. — *S. vulgaris.* ta. — *Saxifraga granulata.* a. — *S. tridactylites.* ta. inom kalcitområdet. — *Scheuchzeria palustris.* a. — *Scirpus acicularis.* S. (Svinsjön). — *S. caespitosus.* Fjällmossen. — *S. Hudsonianus.* Gårdsjön, Torstugan, Getsjön p. 127, Älgsjöterrängen, Raggan, Stavsjömossen, Kranken. — *S. lacustris.* a. — *S. mamillatus.* Fjällmossen. — *S. maritimus.* ta. vid Bråviken. — *S. multicaulis.* Viken 500 m ssv. »L» i L. Älgsjön. — *S. palustris.* a. — *S. pauciflorus.* Svartkärr. — *S. planifolius.* Gästgivargården. — *S. silvaticus.* ta. — *S. Tabernaemontani.* Bråviken vid Svinstaskär och Porsgata. I lertag vid Timmergata. — *S. uniglumis.* Svinstaskär, Prästgården. — *Schleranthus annuus.* a. — *Scorzonera humilis.* ta. — *Scrophularia nodosa.* a. — *Scutellaria galericulata.* a. — *S. hastifolia.* Svinstaskär. — *Sedum acre.* a. — *S. album.* ta. — *Sedum annuum.* ta. — *S. rupestre.* Sandviken (sann. förv.), Marmorbruket. — *S. sexangulare.* Bodaviken, Fagervik, Uttersberg, Oxåker. — *S. telephium.* a. — *Selinum carvifolia.* ta. — *Senecio silvaticus.* ta. — *S. viscosus.* ta. — *S. vulgaris.* a. — *Serratula tinctoria.* ta. (En helbladig form funnen mellan Uttersberg och Dragtorpet). — *Seseli Libanotis.* Marmorbruket, Krokek stn. — *Sesleria caerulea.* S. — *Setaria viridis.* Getå, Sandviken, Fagervik, Eketorp, Gullvagnen. — *Sieglingia decumbens.* a. — *Silene Cucubalus.* ta. — *S. dichotoma.* Erlandstorp, Marmorbruket, Oxåker, Hyttan, Rotnäs, Strömsfors. — *S. nutans.* ta. — *S. rupestris.* Sjövik, Fagervik, Kopparbostigen, Kopparbo, Brandstegen, Skräddartorp, Gårdsjöterrängen, Betlehem. — *Sinapis arvensis.* a. — *Sisymbrium officinale.* ta. — *Sium latifolia.* Sandviken, Frisäter, Fagervik. — *Solanum dulcamara.* ta. — *S. nigrum.* Getå, Frisäter, Fagervik. — *Solidago virgaurea.* a. — *Sonchus arvensis.* a. — *S. asper.* ta. — *S. oleraceus.* a. — *Sorbus aucuparia.* a. — *S. intermedia.* ta. — *Sparganium angustifolium.* Gårdsjön, Getsjön p. 127, Älgsjöterrängen, Älgsjöavloppet, Gullvagnen, Nöden. — *S. Friesii.* S. (Vik). — *S. minimum.* ta. — *S. ramosum.* ta. — *S. simplex.* ta. — *Spergula arvensis.* a. — *S. rubra.* ta. — *S. salina.* Svinstaskär. — *S. vernalis.* ta. — *Stachys palustris.* ta. — *S. silvatica.* ta. — *Stellaria Alsine.* ta. — *S. graminea.* a. — *S. longifolia.* Munkvägen, Ödebrotten. — *S. media.* a. — *S. nemorum.* Getå. — *S. palustris.* ta. — *Succisa pratensis.* a. — *Symphtum asperum.* Sandviken.

Taraxacum erythrospermum. ta. — *T. vulgare.* a. — *Thalictrum flavum.* Frisäter, Uttersberg, Mörtnäsängen, Kulla, Älgstorp. — *T. minus.* Marmorbruket (v. *Kochii*). — *T. simplex.* Wbg. (Oxtorp), Kbg. (Marmorbruket). — *Thelypteris Dryopteris.* a. —*T. Phegopteris.* a. — *Thlaspi alpestre.* Fagervik, Vik. — *T. arvense.* a. — *T. perfoliatum.* Marmorbruket. — *Thymus pulegioides.* Uttersberg. — *T. serpyllum.* a. — *Tilia cordata.* ta. — *Torilis japonica.* ta. — *Tragopogon pratense.* ta. — *Trientalis europaea.* a. — *Trifolium arvense.* a. — *T. aureum.* ta. — *T. fragiferum.* Bodaängen, Fagervik. — *T. hybridum.* a. — *T. medium.* ta. — *T. montanum.* ta. — *T. pratense.* a. — *T. repens.* a. — *T. spadiceum.* S. (Timmergata). — *Triglochin maritimum.* ta. vid Bråviken. — *T. palustre.* a. — *Trisetum flavescens.* Marmorbruket. — *Trollius europaeus.* ta. — *Turritis glabra.* ta. —*Tussilago farfara.* a. — *Typha angustifolia.* Timmergata, Mörtnäs, Nöden. — *T. latifolia.* ta.

Ulmus glabra. ta. — *Urtica dioeca.* a. — *U. urens.* ta. — *Utricularia intermedia.* a. — *U. minor.* Älgsjöterrängen, Ödekyrkmossen, Stavsjömossen, Kranken. — *U. vulgaris.* Prästgården, Kulla, Strömsfors, Rödkärr, Älgstorp, Vik.

Vaccinium myrtillus. a. — *V. oxycoccus.* a. — *V. uliginosum.* a. — *V. Vitis-idaea.* a. — *Valeriana officinalis.* ta. — *V. sambucifolia.* Getå, Kopparbo, Timmergata, Algutsbo. — *Valerianella Locusta.* Svinstaskär, Erlandstorp, Serveringsberget, Bodaviken, Fagervik, Kopparbo, Timmergata. — *Verbascum nigrum.* Kopparbostigen, Kopparbo, Orrekullen, Mörtnäs. — *V. thapsus.* ta. — *Veronica agrestis.* a. — *V. Anagallis- aquatica.* Munkvägen. — *V. arvensis.* a. — *V. Beccabunga.* ta. — *V. chamaedrys.* a. — *V. hederifolia.* Bodaviken, Frisäter, Fagervik, Kopparbo. — *V. officinalis.* a. — *V. scutellata.* a. — *V. serpyllifolia.* a. — *V. spicata.* Erlandstorp*, Kbg. (Gästgivargården). — *V. verna.* ta. — *Viburnum opulus.* ta. — *Vicia angustifolia.* Strömsfors, Böksjötorp. — *V. cassubica.* ta. — *V. cracca.* a. — *V. dumetorum.* Orrekullen*, Marmorbruket, Kopparbo. — *V. hirsuta.* ta. — *V. lathyroides.* Erlandstorp. — *V. pisiformis.* Orrekullen.* — *V. sepium.* a. — *V. silvatica.* ta. — *V. tetrasperma.* ta. — *Viola arvensis.* a. — *V. canina.* a. — *V. hirta.* a. — *Viola mirabilis.* Fagervik, Kopparbo, Timmergata, Prästgården, Orrekullen, Holmtorp, Oxåker, Stentorp. — *V. odorata.* Erlandstorp, Orrekullen, Kopparbo, Gästgivargården. — *V. palustris.* a. — *V. riviniana.* a. — *V. rupestris.* Orrekullen, Hyttan, Ervastekärr. — *V. tricolor.* a. — *Viscaria vulgaris.* a.

Woodsia ilvensis. ta.

Zannichellia palustris. Porsgata, Rödkärr.

Zusammenfassung.

Die Gefässpflanzen der Gemeinde Krokek. Ein Beitrag zur Kenntnis der Flora von Kolmården, Mittel-Schweden.

Eine Untersuchung über die Verbreitung der wildwachsenden Gefässpflanzen in der Gemeinde *Krokek* (93 km² und etwa 16° 20′

ö. L. und 58° 40′ n. B.) von der Provinz Östergötland ist unternommen worden.

Insgesamt sind 727 Species gefunden worden, wozu kommen das Vorhandensein in öffentlichen Herbarien und Literaturangaben von weiteren 43 Species. Die Verbreitung ist bezeichnet mit a. für häufig, ta. für zerstreut (mehr als acht Fundstätte gefunden) und sonst durch Angabe der Fundstätte. Die heutige Verbreitung von *Pleurospermum austriacum* ist besonders hervorgehoben worden.

Neue nordöstliche Vorposten für *Quercus petraea* und *Scirpus multicaulis* sind gefunden worden. Ferner sind solche für *Arnica montana, Cirsium acaule, Hypochaeris radicata, Leontodon hispidus, Pedicularis silvatica* und *Rubus Bellardii* bestätigt worden.

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VEGETATION BELTS OF THE EAST AFRICAN MOUNTAINS.

BY

OLOV HEDBERG.

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Introduction.

The major part of East Africa consists of rather flat highlands at an elevation of between 1000 and 2000 m, which are connected with the highlands of Rhodesia to the south, being separated from the mountains of Abyssinia to the north-east by the depression round the basin of Lake Rudolph. Across these highlands run from north to south the two main branches of the Great Rift Valley, the formation of which begun in the upper Cretaceous (cp. GREGORY 1921 p. 358). Along the faults of the Rift Valley there appeared an intense volcanic activity, and so in due course a number of high volcanic peaks were formed. — Whereas the surrounding highlands are mostly covered by savanna or scrub of different types, the mountains harbour a series of different vegetation zones, as montane rain-forest, bamboo, ericaceous zone, and »alpine» zone. The biotas of their higher parts contain isolated and comparatively small populations of many species, which must presumably at one time have had a more continuous distribution, and which provide good examples of species differentiation.

The occurrence of such a number of isolated high mountains in a tropical climate seems to be something quite unique, and thus East Africa presents very favourable opportunities to study the effects of geographical isolation on different groups of plants and animals.

In 1948, a Swedish zoologic-botanical expedition set out for East Africa from Uppsala under leadership of Dr. Å. HOLM to study species differentiation. The members were four zoologists: Dr. ÅKE HOLM (spiders and insects), Dr. BENGT LUNDHOLM (mammals). Mr. STIG LINDROTH (*Crustacea* and other lake fauna), and Mr. BENGT EKSTRÖM (birds); and one botanist, the present author. The expedition was joined by the zoologist Mr. TORD ANDERSSON from

Gothenburg and his wife Mrs. Gunborg Andersson. During most of the time, we worked in three different groups, each having its special scopes. Dr. Holm and the present writer formed an »alpine group», studying in the first place the alpine fauna and flora of the high mountains. Some results of the work of that group are embodied in this paper; a brief account of the expedition has been published earlier in Swedish (Holm 1949, Lundholm 1949, Hedberg 1949). A short description of the vegetation belts of the mountains was given by the present author in a paper read at the VII International Botanical Congress in Stockholm 1950 (Hedberg 1951).

The mountains visited by the »alpine group» were: Mt. Elgon (Februari, May), Ruwenzori (March—April), Kilimanjaro (June), Aberdare (July), and Mt. Kenya (July—August); cp. map Fig. 1. After the other members of the expedition had returned home, I visited alone Muhavura (October) and Meru (October). In addition, a few collections were made in passing on Mt. Debasien (Kadam), Mau Range, and in the Usambara Mts. near Amani. — On Mt. Elgon, we found opportunity to study also the lower vegetation zones, but on the other mountains we had to concentrate chiefly on the higher parts and could study the Montane Forest Belt only on our way up and down. — The travels between the mountains were made by car, but to get up into the higher parts we had to depend on head porterage.

The plant collections made during the expedition comprise of vascular plants c. 1500 numbers, mosses 1000, liverworts 250, and lichens 500 numbers. The collection of vascular plants comprises 4 sets, which after determination will be distributed to »Universitetets Botaniska Museum, Uppsala»; »Naturhistoriska Riksmuseets Botaniska Avdelning, Stockholm»; »Coryndon Memorial Museum, Nairobi»; and »The Herbarium, Royal Botanical Gardens, Kew». A fifth (incomplete) set will be given to »Universitetets Botaniska Museum, Lund». — The cryptogams will as far as possible be distributed in the same way.

As a basis for the description of the vegetation belts a short account will be given here of the physical features of each mountain district investigated. The way of approach and the points visited will also be mentioned. — A more comprehensive account of the high mountains of East Africa and of Abyssinia, containing detailed descriptions of their exploration history, has recently been published by Jeannel (1950).

Physical Features of the Mountain Districts Investigated.

A. Virunga Volcanoes (Muhavura).

Across the eastern part of the western branch of the Great Rift Valley (cp. Gregory 1921) there lies about 200 km S. of Ruwenzori and 150 km S. of the Equator a chain of volcanic mountains, the Virunga Volcanoes (cp. Fig. 1), well known as the home of the Mountain Gorilla. Over lava plains of recent origin there protrude a number of volcanic cones, two of which are still in an active state. They are arranged in three groups, comprising 8 main peaks. Their names are from east to west: Muhavura (4127 m), Mgahinga (3474 m), and Sabinio (3634 m) in the Eastern group, on the border between Uganda and Ruanda-Urundi; Wissoke (3711 m), Karissimbi (4507 m), and Mikeno (4437 m) in the Central group; Ninagongo (or Nyiragongo, 3470 m) and Namlagira (or Nyamuragira, 3056 m) in the Western group. (Altitudes according to Robyns 1948 a.) The last two, which are surrounded by vast lava fields of different age, were very active a couple of years ago, Ninagongo sending a lava stream down to Lake Kivu, which cut off the main road. Of the other cones Mikeno and Sabinio are rather old and their craters have been destroyed by erosion, whereas the remaining four all possess craters at the top and seem to be fairly new. — The Virunga Volcanoes all appear to have originated after the Rift Valley got its definite form (Robert 1946 p. 117). — For further details about the topography of the mountains, and maps, reference may be given to Mildbraed 1914, Robert *op. c.*, Robyns *op. c.*, and Jeannel 1950. Regarding the names of the mountains and their derivation see Gyldenstolpe 1924 p. 3—6.

The climate of the Virunga Volcanoes is very wet. The rainfall is reported to be greatest at a level of c. 2200—2400 m, where it attains 2250—2400 mm a year. At an altitude of 3000 m the annual precipitation is about 1500 mm, and at the summit of Karissimbi (4507 m) it averages about 950 mm (Robyns *op. c.*, p. 9; cp. Scaëtta 1934). The relative humidity of the air is usually very high, as on Ruwenzori, though sometimes there may certainly occur a spell of dry weather (cp. below p. 180). Snow or hail often falls on the higher parts, but it does seldom remain long.

The nature is rather diverse on the three main groups of volcanoes, owing to edaphic differences. Thus the vegetation on the

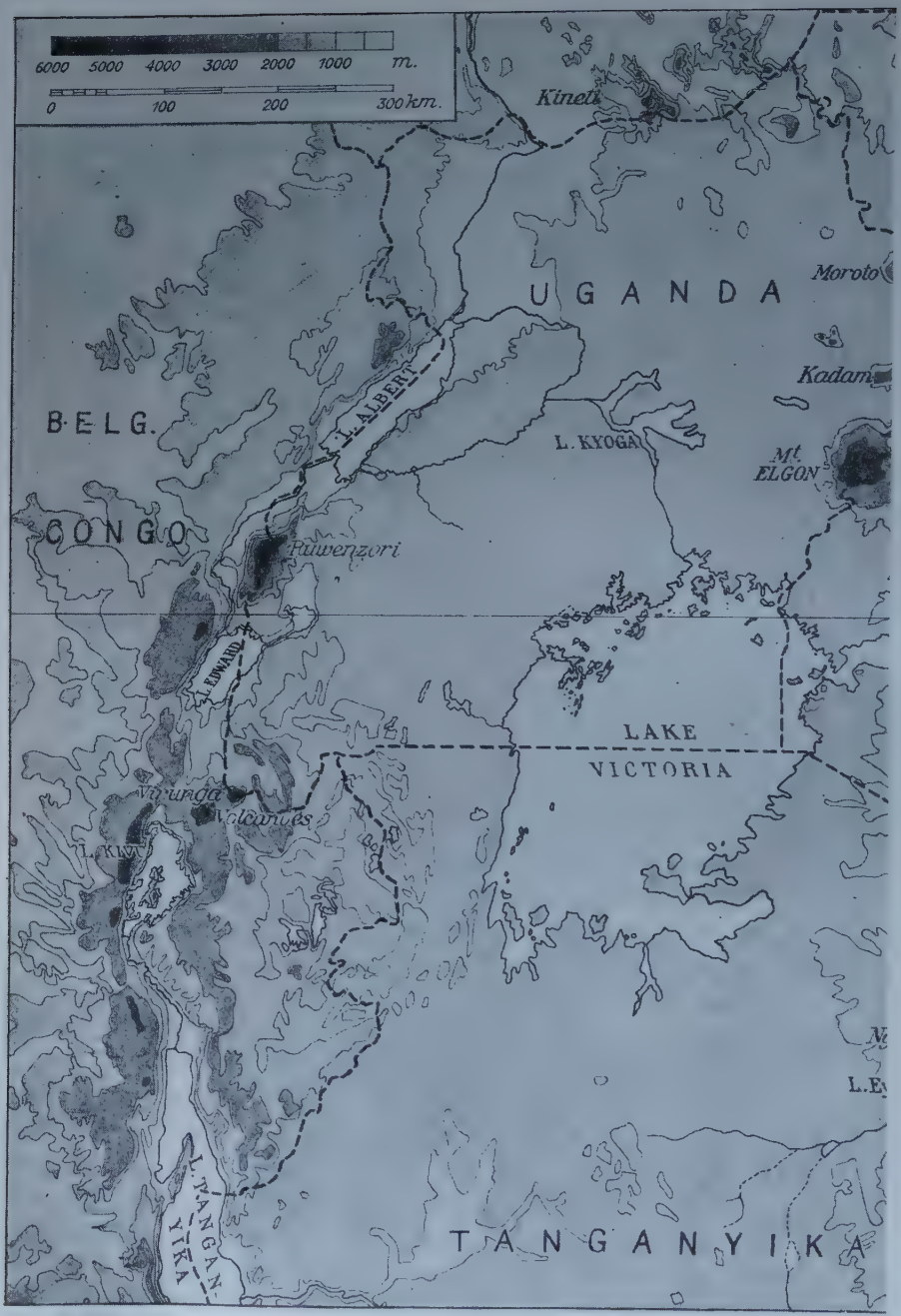


Fig. 1. Map of Equa-

torial East Africa.

young lavas of the W. group differs considerably from that of the older soils of the Central and E. groups (cp. Robyns 1948, with vegetation map). The flora of the different mountains appears, however, to be more or less the same (cp. Mildbraed 1914 p. 649, Burtt 1934 p. 165), as may be expected from their close association. From that and other reasons my studies here were confined to Muhavura, the easternmost one, which is shaped as a perfect cone, possessing at the summit a small crater with a little crater lake about 30 m wide. From the highest part radiate a number of ridges, separated by narrow valleys or ravines, which are often 50 m deep and usually carry a small stream at the bottom.

The ascent was made from the NW. slope, starting from the camp of Mr. Schandl, who was then working with an irrigation scheme for the Government, and who kindly helped me to arrange the safari. A camp was established in the Ericaceous Belt at about 3400 m on the W. slope. It may be mentioned, that the mountain slope is so steep, that no horizontal space big enough for a small tent could be found on the higher slopes below the crater rim, but we had to cut out an earth terrace for it. In this camp I stayed from October 3rd to 10th, devoting most of my time to the Alpine Belt and the upper part of the Ericaceous Belt.

B. Ruwenzori.

Ruwenzori, which is situated between Lake Edward and Lake Albert immediately north of the Equator (cp. Fig. 1), is the largest and most important among the snow-clad mountains of Africa. It is actually a mountain range, comprising six different glaciated groups, named Mt. Stanley, Mt. Speke, Mt. Baker, Mt. Emin, Mt. Gessi, and Mt. Luigi di Savoia, all of which reach more than 4600 m. The highest peak is Point Marguerita on Mt. Stanley, attaining 5119 m. — A number of rivers originate on Ruwenzori, the most important are Mobuku and its tributary Bujuku to the E., Nyamgasani to the S., Butahu, Lusilube and Ruamya to the W., Rwanoli and Lamia to the N.

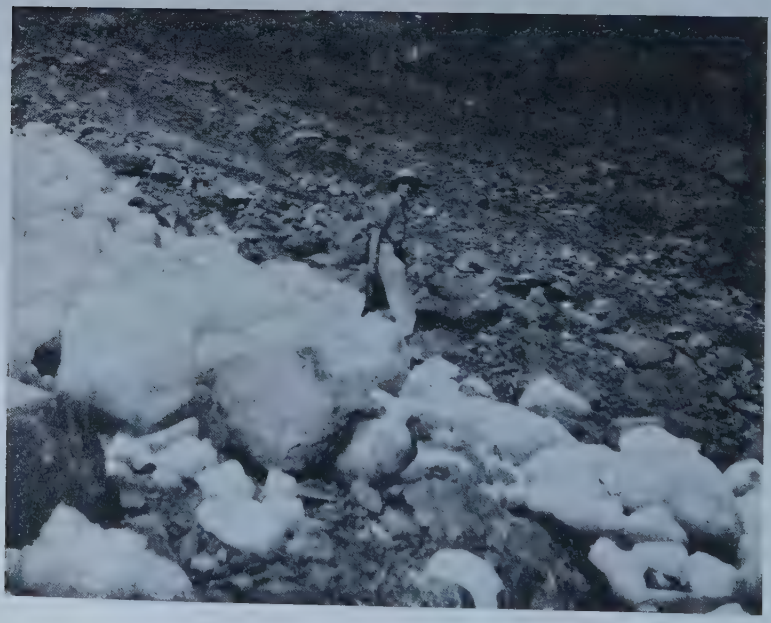
Unlike the other high mountains of East Africa, Ruwenzori is not of volcanic origin, but consists of Archaean rocks, as granite, gneiss, hornblende etc. (cp. Michot 1937 p. 207 and »Carte No 17»). It may be regarded as a fault block, which was left standing, or perhaps lifted, when the surrounding parts subsided at the formation of the Western Rift Valley (cp. Gregory 1921 p. 264).

The present-day glaciers of Ruwenzori descend to about 4200—4350 m on the W. side of the range (Michot *op. c.*, p. 225). On the E. side, they do not reach so far down; thus we found the lowest point of the glaciers at about 4550 m on the E. side of Mt. Speke and probably about the same on the SE. slope of Mt. Gessi (where the actual rim of the glacier could not be reached because of a precipice). On the SW. slope of Mt. Speke the glaciers descend to 4400 m. This divergence is probably due to differences in precipitation, caused by differences in moisture content of winds from E. and W. (cp. below). — Regarding the type of glaciation we may quote: »The glaciers are of the so-called equatorial type, that is, they are more truly ice-caps than ice-rivers; movement is very slight, as is shown by the unusual clearness of the streams (which lack altogether the turbidity of the alpine glacier water) and the absence of large moraines» (Bere, in Bere and Hicks 1946 p. 84). — To this may be added, that when the glaciers end above a precipice, which is quite usual, they now and then break up at the rim and let down an avalanche of huge ice-blocks. In April 1948 we saw — and heard — such an avalanche coming down from the Marguerita glacier, and we could study the iceblocks resulting from another on the SW. slope of Mt. Speke (Fig. 2). These observations indicate, that the glaciers do move a little, anyway (cp. Troll und Wien 1950). In former days they have certainly regenerated below the steeps (cp. e. g. Uhlig 1904 p. 642), though now the ice-blocks rapidly melt away. The glaciers seem to be rapidly diminishing on Ruwenzori as on Mt. Kenya and Kilimanjaro (cp. Bere *l. c.;* Jeannel 1950 p. 26).

The extent of glaciation on Ruwenzori during the pluvials is as yet imperfectly known. In the Mokubu valley powerful moraines have been found down to about 1980 m (Nilsson 1932 p. 26 and Fig. 20). The earlier reports on traces of glaciation on still lower level must, however, be discarded (*op. c.*, p. 24). The higher parts of the mountain have largely been modelled by the ice, showing glacial valleys, glacial »cirques», etc. (cp. Michot *op. c.*, p. 226—230).

The mountain slopes are usually very steep, and the valleys are deep and narrow. The valley bottoms are often divided into series of terraces, which were largely cleared from débris by the pluvial glaciers. Many of these terraces were originally occupied by lakes, most of which have now silted up, giving rise to flat bogs. — For further details about the higher parts of Ruwenzori, reference may

a



b

Fig. 2 a, b. Avalanche of ice-boulders below a glacier on the SW. slope of Mt. Speke, Ruwenzori, altitude c. 4175 m. Many of the ice-boulders were more than half a metre across (cp. the man in the lower figure). In the next surroundings there was no vegetation at all, apparently because of more or less regular avalanches (cp. p. 147). — Photos Å. Holm (upper) and O. Hedberg (lower) 23.3. 1948.

be given e. g. to the beautiful book of the Belgian expedition 1932 (DE GRUNNE, HAUMAN, BURGEON, et MICHOT 1937), containing numerous maps and other illustrations, to BERE and HICKS 1946, and to JEANNEL 1950.

The climate of Ruwenzori is singularly wet and cloudy. Thus the higher parts can only very rarely be seen from the plains below, since they are almost constantly hidden by clouds. And a spell of sunshine up there does never last longer than a few hours. As stated by DAWE (1906): »On the upper region of the mountain rain falls almost daily in the form of heavy mists, and the vegetation throughout the day is usually dripping with moisture.» — The driest parts of the year are said to be about Mid-summer and Christmas (cp. SYNGE 1937). — The annual precipitation is estimated to reach a maximum value of c. 4000 mm at an altitude of 2200 m on the W. slopes, whereas the highest parts probably get something round 1600 mm (SCAËTTA 1934 p. 245—246). On the E. slopes the precipitation is certainly less, though no figures are available.

Our ascent of Ruwenzori was made from the east following the usual route from Bugoye, where excellent porters were obtained, along Mobuku and Bujuku rivers (cp. maps in BERE and HICKS 1946 or DE GRUNNE *et al.* 1937). Our base camp was placed at Bigo (or Kigo) at c. 3450 m, from where we studied the upper part of the Ericaceous Belt on the surrounding mountain slopes. The higher parts were studied from temporary camps in the upper parts of Bukurungu valley and Mijusi valley (which branch off to the north from Bujuku valley), at »Cooking pot» above Lake Bujuku, and at Kitandarai (i. e., at the S. one of the two lakes c. 2 km S. of the Scott-Elliot pass). The descent was made from Kitandarai over Freshfield pass to Mobuku river and then down along Mobuku valley. — Our Ruwenzori trip lasted from March 18th to April 13th.

C. Mt. Elgon.

Mount Elgon is situated on the border between Kenya and Uganda about 120 km NE. of Lake Victoria (cp. Fig. 1). It is an extinct volcano of tertiary origin, possessing a giant crater — or rather caldera (ÖDMAN 1930 p. 464). The lower parts of the mountain ascend rather slowly, though precipices (»bluffs») occur in places to the N., W., and S. From the mountain radiate a number of spurs, separated by narrow ravines. A sketch map of the mountain has

been provided by Ödman (*op. c.*, p. 536, cp. Nilsson 1932 p. 8). The higher parts of the mountain, which are often rather steep, have been mapped by Nilsson (*op. c.*, Pl. I, II). The caldera is ovate, measuring about 8 × 7 km, and is surrounded by a marked rim. It is drained by a small river, Swam, which runs out through a steep valley towards NE. In the lower part of the crater close to the outlet there is a hot spring, called »Maji ya moto» (3580 m above sea-level), the water of which carries much H_2S (cp. Nilsson *op. c.*, Pl. I). — Most of the caldera lies between 3550 and 3900 m, whereas the crater rim usually exceeds 4000 m, the highest point reaching 4315 m (Lovén's Peak, according to Nilsson *l. c.*). Of the other named summits, Jackson's Peak attains 4175 m and Koitobbos 4215 m.

At present there are no glaciers on Mt. Elgon, but during the pluvials, the mountain was abundantly glaciated. The extent of the former glaciation has been traced by means of moraines and pinnacles (Nilsson *op. c.*, Pl. III, map).

Straight across the caldera from E. to W. goes a path, the »Wagishu track», passing the crater rim on the N. slope af Koitobbos to the east and in the »Uganda pass» (3895 m) to the west (cp. Nilsson *op. c.*, Pl. I). Along this track there is quite a lively traffic of natives and cattle, which must certainly influence the alpine flora and fauna to some degree (cp. p. 191).

Meteorological data from Mt. Elgon are very scarce. At an altitude of c. 2000 m the annual precipitation is reported to be about 1200—1300 mm (45—50 in.) on the E. slopes and 1500 mm (60 in.) to the W. (Lugard 1934). In the forest belt the rainfall has been estimated to similar values (Dale 1940), but from higher altitudes nothing seems to be known. — For further particulars the reader is referred to the above-mentioned papers, especially Nilsson 1932, and to Johnston 1902, Dummer 1919, and Lugard 1934.

During our visits to Elgon, we had our base on the farm Kaptega estate c. 15 km NW. of Endebess. From there we studied the savanna on the foot-hills and the montane forest in Februari and March. In May, we studied the Alpine Belt, ascending from our base against Koitobbos and then along the wagishu track into the crater. Here we camped from May 12th to 22nd at Maji ya moto, from where excursions were made to various parts of the crater, i. a., most of the different peaks on the crater rim.

D. Aberdare.

Aberdare is a long mountain range with soft outlines, situated at the border between the Laikipia High Plateau in the east and the Great Rift Valley in the west (cp. Fig. 1). It is about 100 km long from north to south, its N. end coming very close to the Equator. Most of the mountain is formed by gently undulating highlands at an altitude of about 3000 m, over which rise a couple of conspicuous peaks, Sattima (3875 m) to the N. and Kinangop (3906 m) to the S. In these highlands the rivers have in many places cut down deep valleys, sometimes canyons, in the rock. The mountain is certainly of volcanic origin and seems to be of about the same age as Mt. Kenya (Gregory 1921 p. 105). — No traces of former glaciation have been reported (cp. Jeannel 1950 p. 123).

The literature about Aberdare seems to be remarkably scarce; apparently the mountain has been largely neglected by naturalists and tourists in favour of its taller neighbour to the east, Mt. Kenya. However, its flora, together with that of Mt. Kenya, has been treated in a number of publications by Rob. E. Fries and Thore C. E. Fries (see bibliography in Fries and Fries 1948 p. 81) and its fauna studied by Alluad and Jeannel (cp. Jeannel 1950).

The climate of Aberdare is rather wet, though as yet little is known about the magnitude of the precipitation. In 1948, however, a series of gauges were installed at different altitudes, so in a few years we may have reliable mean values for the precipitation. The values for the first year (18/3 1948—18/3 1949), which have been obtained from the East African Meteorological Department, would indicate an annual precipitation of c. 1500—2000 mm for the stations on the E. slopes between 1800 and 2600 m altitude. A gauge at about 3300 m altitude seems to give about the same value, though here the available figures do not even comprise one year.

When ascending Aberdare, we started from Nyeri. Donkeys and boys for our transports were kindly supplied by the Forest Department. We advanced along a well-cut track through the rain-forest and bamboo (»the Nyeri track»), which goes from Nyeri across the mountain towards »Kinangop Plateau» (cp. Jeannel 1950 p. 120). Our main camp was placed on the moorlands c. 15 km north of Kinangop Peak, at an altitude of c. 3100 m. From here the surrounding parts were investigated, especially Kinangop, which was visited three times. Our stay on the mountain lasted from July 10th to 21st.

E. Mt. Kenya.

Mount Kenya is situated about 140 km NNE. of Nairobi and 440 km from the coast, its northern slopes being cut by the Equator (cp. Fig. 1). It is the second highest mountain of Africa, the highest of its twin peaks (Batian) attaining 5195 m. The mountain represents the remnants of an ancient volcano. To quote from one of its early explorers: »It consists in its lower parts of a huge pile of volcanic ash and débris, with a low gradient, rising from 7200 to 10,200 feet (i. e. 2200—3100 m), densely covered with forest and bamboo djungle. Above this frown steep craggy slopes of coarse agglomerates, ash, and lava, while the whole is surmounted by a rugged pyramidal peak which is part of the central core of the old volcano» (Gregory 1894 b, p. 515). Rock specimens collected at the summit by Mackinder (cp. Mackinder 1900) proved to be the same nepheline-syenite as most of the central peak, showing that the existing summit must be far below the floor of the original crater, which must have been destroyed by at latest the pliocene (Gregory 1921 p. 144). The surrounding zone of lava, tuff and agglomerate is to be regarded as remnants of the foundation of the crater walls (Gregory *op. c.*, p. 146).

From the steep central peak there radiate a number of big valleys (cp. Gregory 1894 a, and Nilsson 1932 p. 19, map). The largest one to the west is Teleki valley; then follow, counting clock-wise: Buguret v., Hausburg v., Mackinder v., Hinde v., Gorges v., Hobley v., and Nairobi v. (Höhnel v.). The upper parts of the valleys are mostly beautifully U-shaped by glacial erosion, whereas the lower parts are V-shaped. The ridges between them are often crowned by sharp pinnacles, formed by weathering of the loose agglomerates (cp. e. g. Gregory 1921 Pl. XII, XIV).

Although Mt. Kenya is situated practically on the Equator, it harbours a number of glaciers, the most important of which are Lewis glacier, Darwin gl., and Tyndall gl. to the W.; and Gregory gl. to the E. Nowadays, the glaciers descend to about 4400 —4540 m (14,450—14,900 ft.) on the W. and N. slopes (Mackinder 1900), and to c. 4700 m to the E. (Nilsson *op. c.*, p. 21).[1] The glaciation seems

[1] Nilsson (*op. c.*, p. 22) gives an altitude of 4700 m also for the lower ends of the W. glaciers, adopting Gregory's figure. According to Mackinder (*op. c.*, p. 483), however, the margins of the Tyndall and Lewis glaciers lie at 14,820 and 14,850 ft., respectively (i. e. 4520 and 4530 m). Mackinder's altitude determinations seem to be more

to be much more intense on the W. side than on the E., which may partly be caused by differences in precipitation, but is certainly also largely due to variations in cloudiness. Thus in the early part of the day, the sky is most often clear at this altitude, whereas about noon the cloudiness will usually increase. Accordingly the E. side is much more exposed to the sun, and so the ablation here is more intense (Troll und Wien 1950). — During my stay on the mountain I found this diurnal cycle in cloudiness to be most regular (cp. also Jeannel 1950 p. 107).

The former extent of glaciation on Mt. Kenya has been studied by Gregory (1894 b), Mackinder (1900), and Nilsson (1932). Old moraines have been found down to 2990 m in Teleki valley on the W. side (Gregory *op. c.)*, and 3050 m in Gorges valley on the E. side (Nilsson *op. c.*). The latter found evidence of at least two different glaciations. Jeannel (1950 p. 105) reports moraine boulders from an altitude of about 2850 m in Buguret valley towards WNW.

The upper parts of the valleys give good examples of glacial cirques and troughs, as figured in the above-mentioned papers (e. g. Mackinder *op. c.*, p. 473; Gregory 1921 Pl. XIV: b). In these occur a number of lakes or tarns, the most important being Lake Höhnel in the upper part of Nairobi valley, Lake Michaelsson in Gorges valley, and Lake Teleki in Teleki valley. On the ridge north of the upper part of Teleki valley, there are two small tarns and a hut; the place is called »Two tarn col».

The annual rainfall is rather high over the whole mountain. On the lower slopes it appears to be highest on the NE. side, reaching 2700 mm at an altitude of c. 1700 m (Troll und Wien *op. c.*). In the forest belt it is said to be about 750—1000 mm in the N. and W., and probably 1250—1500 mm to the S. and E. (Gardner in Rendle 1932). At about 3100—3500 m on the NW. side it ranges between 750 and 1750 mm (figures obtained by courtesy of the East African Meteorological Department), though so far no good average values are obtainable. Also in the Alpine Belt the precipitation seems to be rather high, and probably more evenly distributed over the year (Troll und Wien *op.* c.).

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reliable (cp. discussion in Mackinder *op. c.*, p. 476 ff.), though as he calculated his values on the basis of a height of 17,200 ft. (5250 m) for the peak, they should be reduced by about 50 m. — Our measurements gave c. 4500 m for the rim of Tyndall glacier, and Troll und Wien (1950 p. 258) give 4475 m for the lowest part of Lewis glacier.

We ascended the slopes of Mt. Kenya from the west, making use of the facilities offered by the »Kenya Mountain Safaris, Ltd». The route followed chiefly Teleki valley, and our main camp was established in the higher part of that valley at an altitude of about 4200 m. From there excursions were made i. a. to the Tyndall and Lewis glaciers, to Lenana Point, and to the upper parts of the surrounding valleys (Buguret, Hausburg and Nairobi valleys). The ascent was started on July 24th, the time between July 26th and August 17th was spent in the Alpine Belt, and on the way down I stayed from August 18th to 22nd in a camp in the Bamboo Zone.

F. Kilimanjaro.

Kilimanjaro, which is situated in Tanganyika Territory about 280 km inland from Mombasa (cp. Fig. 1), is the highest mountain of Africa, and probably the one that has been most extensively studied. It is of volcanic origin and shaped like a flat dome, possessing 2 different main peaks about 10 km apart, Kibo (c. 5890 m) to the west, and Mawenzi (c. 5193 m) to the east (cp. Pl. IIA; altitudes adopted from JEANNEL 1950 p. 66). Between them is a saddle plateau at a height of about 4400 m (cp. MEYER 1890, 1900; GILLMAN 1923; NILSSON 1932). West of Kibo extends the Shira crest, the highest part of which reaches 3906 m. The three peaks mentioned represent three generations of volcanic activity, Shira the oldest, and Kibo the youngest. Whereas the older two have been largely destroyed by erosion, Kibo is a perfectly shaped cone with a caldera, caused by subsidence and about 2 km wide, in the centre of which there is a small secondary eruption cone with its own crater (cp. MEYER 1900, RICHARD 1945, SPINK 1945, and JEANNEL 1950 p. 83). — There are many indications, that the volcanic activity does not lie very far back in time; thus MEYER (1900 p. 165) found glacio-fluvial material covered with lavas on the Galuma Plateau, and on the »Lavahügel» (cp. map in MEYER *op. c.*) in the S. part of the saddle the surface structure of the lava streams seems remarkably fresh (author's observations). Besides, fumarolic activity has recently been reported from the crater of Kibo (RICHARD *op. c.*, SPINK *op. c.*).

The present-day and former glaciations on Kilimanjaro have been studied by a number of explorers; a recent review is given by NILSSON (1932 p. 28—39). The most extensive glaciation on Kibo

nowadays is on the SW. side, where the glaciers in 1898 reached down to about 4000 m, whereas on the NE. side they only reached 5700 m (Meyer 1900), the differences being attributed to differences in moisture content of the winds from different sides and hence in precipitation (Meyer *op. c.*, Nilsson *op. c.*; cp. also p. 153 above and Spink *op. c.*, however). The glaciers are rapidly melting away (cp. Gillman 1923, Spink *op. c.*); on the SW. slopes of Kibo they only reached down to 4500 m 20 years ago (Nilsson *op. c.*, p. 32; cp. also Jeannel 1950 p. 84). On Mawenzi there are no glaciers. — The pluvial glaciation on Kilimanjaro seems to have reached down to about 3600—3800 m over most parts of the mountain (cp. Meyer *op. c.*, Nilsson *l. c.* and Fig. 31).

The S. slope of Kilimanjaro rises very gently, whereas the N. side is a little steeper. The ascent along the usual route above Marangu is easy, since the erosion valleys are not very deep here. In many places on the lower slopes, however, the streams have cut down deep gorges in the soft volcanic material, making it a very difficult task to go round the mountain at that altitude (Moreau 1936 p. 845). The only parts which are really difficult of access are the peaks of Mawenzi.

The climate of Kilimanjaro has been described e. g. by Klute (1920) and Moreau (1936). From the latter we may quote: »It certainly appears, however, that on any given line drawn down the slope of the mountain the lower part of the forest belt receives most of the precipitation, which is supplemented by the frequent cloud-layer of that belt. Above the forest there is reason to believe that the rainfall is much reduced, while below, as the cultivated zone is traversed and the last slopes are descended, the rainfall is known to decrease very rapidly on both Kilimanjaro and Meru.» — Immediately below the forest belt, the precipitation seems to vary between 750 mm (30 in.) and 2500 mm (100 in.), being highest to the S. and lowest to the NW. and N. (Moreau *op. c.*). — From 1945 there have been installed a number of rain gauges at higher altitudes, and the values so far obtained (communicated by the East African Meteorological Department) do indicate a definite maximum somewhere in the Montane Forest Belt, whereas there is a very considerable decrease in rainfall towards the summit. Thus in the saddle at c. 4400 m the annual precipitation appears to be of the order of 300 mm a year, and in the top crater of Kibo it seems to lie far below 100 mm, though here of course most of the precipitation may occur

as rime, and adequate values are hardly obtainable by means of a common rain gauge.

The biotic effects of the low precipitation on the higher parts is accentuated by their edaphical peculiarities. The rock is mostly covered with thick layers of sand and gravel, which let through water very easily. Thus the melt water from the glaciers and much of the precipitation falling on the higher parts sink straight down into the ground, reappearing as wells on the lower slopes. Accordingly, the higher parts are very dry, most of the saddle being a typical desert (Meyer 1900 p. 148, Gillman 1923), containing some small »oasis» where ground water comes out.

Our ascent of Kilimanjaro was made along the usual route from Marangu and via the three rest-houses Bismarck Hut, Peter's Hut, and Kibo Hut (cp. e. g. Cotton 1930). Most of the time we devoted to studies of the biota of the southern mountain slopes above 3500 m and the saddle, using Peter's Hut as a base. We also ascended Kibo, reaching Gillman's Point (cp. Richard *op. c.*). Our stay on the mountain lasted from June 13th to 28th.

G. Mt. Meru.

Mt. Meru, which is situated about 70 km WSW. of Kilimanjaro (cp. Fig. 1) appears to be a volcano of fairly recent origin. From an irregularly ovate base, measuring about 35 × 80 km at an altitude of 1500 m, the mountain rises rather steeply to 4566 m (acc. to »Map of Kenya Colony» in 1 : 2 000 000). From the W. side it seems to form a perfect volcanic cone, but actually the eastern part of the crater wall was long ago eliminated by some gigantic explosion (cp. Jaeger 1906 p. 245). In the centre of the old crater there has since been formed a small secondary cone, carrying on its surface lava streams of a very recent-looking texture (Uhlig 1904 p. 717). In December 1910 slight volcanic activity was observed, mainly visible as a column of smoke from the inner crater (Uhlig 1911). The remaining parts of the outer crater wall are rather steep on the outer side (cp. Uhlig 1904 Abb. 65). On the inner side they are almost perpendicular, making it impossible to enter the crater from the west or the south. The streams of the mountain, which at least on the higher parts carry water only occasionally, have eroded rather deep valleys on the slopes, as is well shown on the above-mentioned tele-photo by Uhlig *(l. c.)*.

The soil, which has largely originated from volcanic ashes, has proved to be very fertile on the lower slopes to the south, where the rainfall is great enough to permit agriculture. The lower parts of the other slopes are very dusty, the dry and light soil being easily swept away by the wind (cp. Uhlig *op. c.*, p. 694). Above the forest limit, most of the ground is occupied by a steep scree containing much sand, which evidently lets through water very easily. Accordingly the ground here is very dry and the flora and fauna poor. No place with permanent water could be found above or closely below the forest line.

Sketch maps of the mountain have been provided by Uhlig (*op. c.*, p. 693) and Moreau (1936), and the former has given a short geographical and geological description, which was later supplemented by Jaeger (1906). — The climate of the mountain is rather imperfectly known. According to Moreau (*op. c.*, p. 846 ff.) the precipitation appears to be highest in the lower part of the forest belt and to diminish both above and below the forest. Furthermore, the S. and SE. slopes receive more rain than the N. and W. ones. Thus at Ngare Narok (at an altitude of about 1750 m on the S. slope) the annual precipitation averages 1775 mm (71 in.), while Ngare Olmotoni 5 miles to the W. and at about the same level gets only 850 mm (34 in.), and Arusha lower down on the S. slope 1125 mm (45 in.). The W. and N. slopes are very dry, receiving less than 500 mm (20 in.) at Ol Doinyo Sambu towards NW. and 750 mm (30 in.) on the lower part of the N. slopes. — Snow and hail sometimes fall on the higher parts of the mountain, but it soon melts away and there seems to be no conclusive evidence of earlier glaciations (cp. Uhlig *op. c.*, p. 708), though Sjöstedt (1910 p. 56) mentions glacier-polished rocks and glacial striae from the S. side of the mountain.

My ascent of Mt. Meru was undertaken from SW., starting from Olkakola estate at about 2500 m, where I received generous help in obtaining porters and equipment. My camp was pitched in the upper part of the Ericaceous Belt at about 3400 m. Here I stayed from October 26th to November 2nd, investigating in the first place the Alpine Belt with the summit but also the upper part of the Ericaceous Belt.

II. Altitude Measurements.

One of the main objects of our field work was to determine the altitudinal limits of the »afro-alpine» animals and plants. For that purpose the altitude of every specimen collected was measured, and also the topmost and downmost specimens found of each species possible to distinguish in the field. For the measurements an altimeter of type »Thommen» (Swiss army model) measuring up to 6000 m was used. As these figures will be of considerable importance to our future work, a short account is given here of the methods and corrections used. For the elucidation of the meteorological side of the matter I am indebted to Mr. Niels Rodskjaer, fil. kand.

The figures shown by the altimeter are subject to a number of errors. The instrument is graduated according to an idealized »normal atmosphere CINA», i. e., dry air with a pressure of 760 mm Hg and a temperature of 288° K. at sea level, the temperature decreasing 6°.5 for every 1000 m of altitude, and the acceleration at sealevel being equal to 9.80665 m/sec.^{2} (cp. »*Grundlagen der barometrischen Höhenmessung*»). According to information in a letter from »Thommen Watch Co.», the instruments have been adjusted to show a value 1 % higher than that corresponding to the said conditions. — Thus what the altimeter shows is *not* actual altitude but air pressure, translated directly on the scale of the instrument to the corresponding altitude in such a »normal atmosphere CINA» (with the correction just mentioned). The atmospheric conditions at the Equator are rather different from this ideal case. In the first place, the lower strata are warmer, giving to those parts a lower density, and thus making barometric altitude readings too small. Secondly, the air contains a considerable degree of moisture, causing a deviation in the same direction, since water vapour is lighter than air. Thirdly, the acceleration (g) at the Equator is smaller than 9.80665 m/sec.^{2}, which gives a similar deviation. — Taken together, these factors will produce a considerable error. By means of values for the mean air temperature and dew point temperature at different pressure surfaces above Nairobi for 1948 (figures obtained by courtesy of the East African Meteorological Department), the numerical value of this error could be calculated for different altitudes. In Fig. 3 it has been plotted against the altitude shown by the altimeter. This curve may thus be used for correction of the

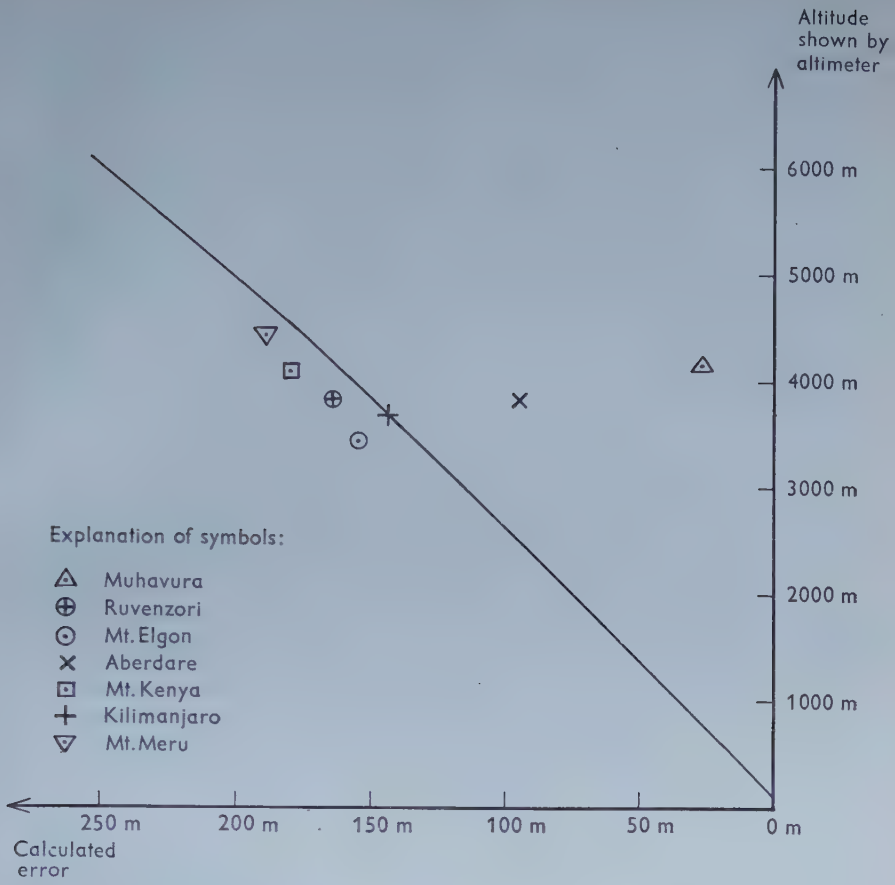

Fig. 3. Error in altimeter readings, resulting from differences in atmospheric and gravity conditions at the Equator as compared with the »normal atmosphere CINA», plotted against altitude shown by altimeter (cp. p. 158). The points represent fixed points, one for each mountain, the altitudes of which were taken as standard (cp. Tab. 1). Owing to different adjustment of the scale of the altimeter at the beginning of the mountain trips, these points fall on different distance from the curve. — Orig.

primary values obtained. However, the uncertainty is still rather large, if no fixed points are available, and the altimeter should not be used to measure absolute heights but only relative ones, where one fixed point is known. Consequently, on each of the mountains investigated such a fixed point was adopted, the altitude of which was known from earlier investigations. All measurements made on the mountain were then correlated to this point, so that only altitudinal differences were measured. These have afterwards been

corrected by help of the curve in Fig. 2. If the adopted value of the fixed point in the future should prove to be erroneous, our measurements are subject to corresponding corrections. The fixed points used and the values adopted for them are shown in Tab. 1.

Of course there are also other sources of error in the measurements. Thus the adjustment of the altimeter to the »normal atmosphere CINA» might not have been correct or the instrument might have turned wrong during the expedition. However, it was controlled in several ways. Firstly, on all the excursions I made together with Dr. Holm, we brought two altimeters of the same kind, which were controlled against each other. Secondly, we made altitude readings for every summit, pass, or camp visited, thus being able to compare afterwards with the recognized altitudes of these places. Thirdly, on the return home my instrument was tested by »System Paulin AB» in Stockholm and found to be correct, giving a maximum deviation of 30 m in 6000 m. When the instrument was used to measure relative altitudes in the way outlined above, this should in no case give an error bigger than ± 10 m. An error of about the same order of magnitude may occur because of »lagging» of the instrument (cp. »*Grundlagen der barometrischen Höhenmessung*» p. 11—12). Finally, some error may arise from the diurnal variation in air pressure and temperature. However, these variations seem to be rather small in equatorial regions. Thus the normal daily variation in pressure keeps within ± 1.7 mm in Congo (Robert 1946 p. 261). The diurnal variations of temperature in the free atmosphere seem to be of the order of 2°—3° in equatorial regions (Haurwitz 1941 p. 105), which may give a maximum error of about 1 % of the altitude difference measured in one day. As the latter difference rarely amounted to 1000 m, the error resulting from this factor will usually be less than 10 m. — The variation of the temperature at the ground is rather considerable, but does not seem to have any great influence on the air pressure, since the differences found when the altimeter was read at different times in a camp at high altitude rarely exceeded 20 m on the scale.

Thus, when all the errors mentioned are considered, the total error of our corrected altitude figures should probably in no case exceed ± 50 m and usually be considerably less than that, in so far as the values adopted for the »fixed points» are correct. The altitudes measured by us have in most cases after the corrections have been applied been rounded off to the nearest 50 m.

In an appendix to Table 1 I have listed the corrected values for some camp sites, huts etc., the altitudes of which seemed to be imperfectly known. The error in the figures is of the order just mentioned.

Tab. 1. Altitudes of fixed points.

1) Muhavura, summit. 4127 m (Robyns 1948).[1]
2) Ruwenzori, Lake Bujuku. 3916 m (de Grunne *et al.* 1937, Carte 15).
3) Mt. Elgon, Maji ya moto (hot spring in the lowest part of the crater). 3580 m (Nilsson 1932, map Pl. I. — Altitude measurements based on the value 14,140 ft. = 4311 m on the Elgon sheet in the series of maps of East Africa in 1 : 250 000. For further details see Nilsson *op. c.*, p. 12.
4) Aberdare, Kinangop Peak. 3906 m (Map of Kenya Colony in 1 : 2 000 000. Geographical Section, General Staff, No 2871. Published by War Office, 1940. 5th Edition 1943.)
5) Mt. Kenya, Lake Höhnel. 4240 m (13,900 ft.; figure communicated by the Mountain Club of Kenya in a letter of 14/4 1950).
6) Kilimanjaro, Peter's Hut. 3815 m (12,500 ft.; reference: same as No 5; 3800 m acc. to Gillman 1923).
7) Mt. Meru, summit. 4566 m (Reference: same as No 4).

Appendix to Tab. 1.

Altitudes obtained by us for some camp sites, huts etc. (cp. above).

Ruwenzori:

Bugoye 1300 m.
Mihunga 2150 m.
Kyanasabo 2980 m.
Bigo 3450 m.
Kitandarai 4025 m.

Elgon:

Kaptega estate 2150 m.

[1] The high original values for that mountain (cp. Fig. 3) depend on high adjustment of the scale of the altimeter after an approximate »fixed point» at Kanaba gap, which is probably incorrectly estimated.

Mt. Kenya:

Top camp of Kenya Mountain Safaris Ltd. (Teleki valley) 4200 m.
Top Hut 4815 m.
Lenana Point 5020 m.

Kilimanjaro:

Marangu Hotel 1400 m.
Bismarck Hut 2800 m.
Kibo Hut 4830 m.
Gillman's Point 5800 m.

III. Vegetation Belts.

The vegetation and flora of the East African high mountains have been studied and described by a number of botanists. Most of these have, however, visited only one or two of the mountains, and in describing the vegetation they have often used a zonal classification which is valid locally but not easily applicable to all of them. Since the mountains are rather different as to climate and vegetation, it is not easy to integrate these different descriptions to a common system. Another difficulty comes from the fact that there are big differences between different sides of the same mountain. Mount Meru, for instance, possesses on its southern slope a luxuriant rain-forest and a bamboo zone, whereas on the north half of the mountain there is no bamboo and the forest zone is much reduced, leaving an open gap to the north (cp. p. 177 below). On Mt. Kenya there are similar differences. Also the zonal divisions and names of the zones suggested for the same mountain by different authors are often rather different, as may be seen from the synonym lists below. — However, a stabilized system of classification for the vegetation zones of all the East African mountains would no doubt be very useful for those concerned with their flora and fauna (cp. e. g. Scaëtta 1934 p. 294, Burtt-Davy 1938 p. 1). Thus, I have tried to work out such a classification, based on observations in the field and on the available literature. This account only deals with the mountain regions visited by the author, i. e., all those in E. and Central Africa which attain an altitude of 3750 m or more. Of course there are several other mountains almost as high, which might deserve to be included in such a study (cp. Fig. 1), e. g. Loolmalasin

(3648 m), Cherungani (3444 m), and Mt. Kineti (3163 m), not to speak of Mt. Cameroon, but neither time nor funds available were sufficient for that.

1. Terminology and Methods.

Regarding the terminology, the word *zone* is used in this paper to denote a more or less local »altitudinal region», the main vegetation of which is clearly distinct from that of the adjacent zones, e. g., the Bamboo Zone described from Mt. Kenya and Aberdare by Fries and Fries (1948 and earlier works). A *belt* is an »altitudinal region», which can be traced on all (or most) mountains of sufficient height in a definite part of the world, as for instance the Montane Forest Belt on the East African mountains (cp. below), though the zones representing it on each mountain may differ as to number and appearance (regarding the terminology cp. e. g. Flahault und Schröter 1910, Du Rietz 1930 b, Braun-Blanquet 1932, Selling 1948).

In bounding the zones of vegetation there are two different ways, provided we keep to the plants and plant communities themselves. We may investigate the vertical distribution of all the species and draw the zone limits where many distribution limits of individual plant species coincide, as was done, e. g., by Sendtner (1854 p. 372) and by van Steenis (1935). Or we may draw the limits according to the plant communities, as has been made by most other botanists. Then again we may consider all or most of the plant associations present, as demonstrated by Braun-Blanquet (1932 p. 348), or we may keep to one or a few plant communities of high rank, »climax formations» according to Clements (cp. e. g. Clements 1916), which are usually founded on the highest stratum present. The last method seems to be the one most often used and most exact, since the distribution of the main plant communities can usually be determined easier and with greater accuracy than that of individual species or plant communities of lower rank. It is also to be preferred from a practical point of view, because it should be possible to recognize the different zones in the field without having to make a detailed floristical analysis. — On the other hand, it seems highly probable, that a division made by the floristical method first mentioned, or by the more exact sociological method, would lead to essentially the same result, since undoubtedly a considerable number of plants and plant associations have their distribution limits more or less coin-

ciding with the main vegetational boundaries. — For further details as to the principles for delimitation of vegetation belts see esp. Schröter (1926 p. 2 ff.) and Du Rietz (1930 a, p. 352 etc.).

There are three vegetational limits, which recur on all the mountains investigated, namely: (1) the lower limit of the montane forest against the savanna or steppe; (2) the limit between the broad-leaved or coniferous montane forest and the ericaceous zone; (3) the upper limit of the continuous ericaceous vegetation. We may, accordingly, distinguish three main vegetation belts occurring on all the mountains, namely (from below):

I) Montane Forest Belt.
II) Ericaceous Belt.
III) Alpine Belt.

The distribution of these belts on the different mountains is schematically represented in Fig. 4. — Below the Montane Forest Belt there occur at some of the mountains remains of Lowland Rainforest, but this has in most cases been destroyed by cultivation (cp. e. g. Volkens 1897, Moreau 1936). That zone will not be treated in this paper, however.

One of the most useful lines of demarcation in the European mountain vegetation is the upper forest limit or tree limit (cp. Schröter *op. c.*). It is not possible to use that limit with the same success in Tropical Africa, because of the occurrence of the Giant *Senecios*, which ascend on some of the mountains almost to the upper limit of vascular plants, and which must undoubtedly be classified as »trees». One should remember, however, that the term »tree», which was used even by the old Greeks, is a very wide concept, covering a multitude of different life-forms (cp. e. g. Du Rietz 1931). The Giant *Senecios* belong to a very specific life-form, peculiarly adapted to the »afro-alpine» climate, which cannot be homologized with the trees of the subalpine zones of Europe. (The »afro-alpine» life-forms will be treated in a further publication.) The »forest limits» or »tree limits» of Tropical Africa and Europe are thus by no means homologous (cp. Schmucker 1926). The big climatic differences between the »alpine» zones of high and low latitudes have been stressed especially by Troll (1948).

The danger of using the tree limit as a basis for classification of altitudinal zones in East Africa is clearly shown in the system used by Engler (1925). If we pick out for instance the vertical distribu-

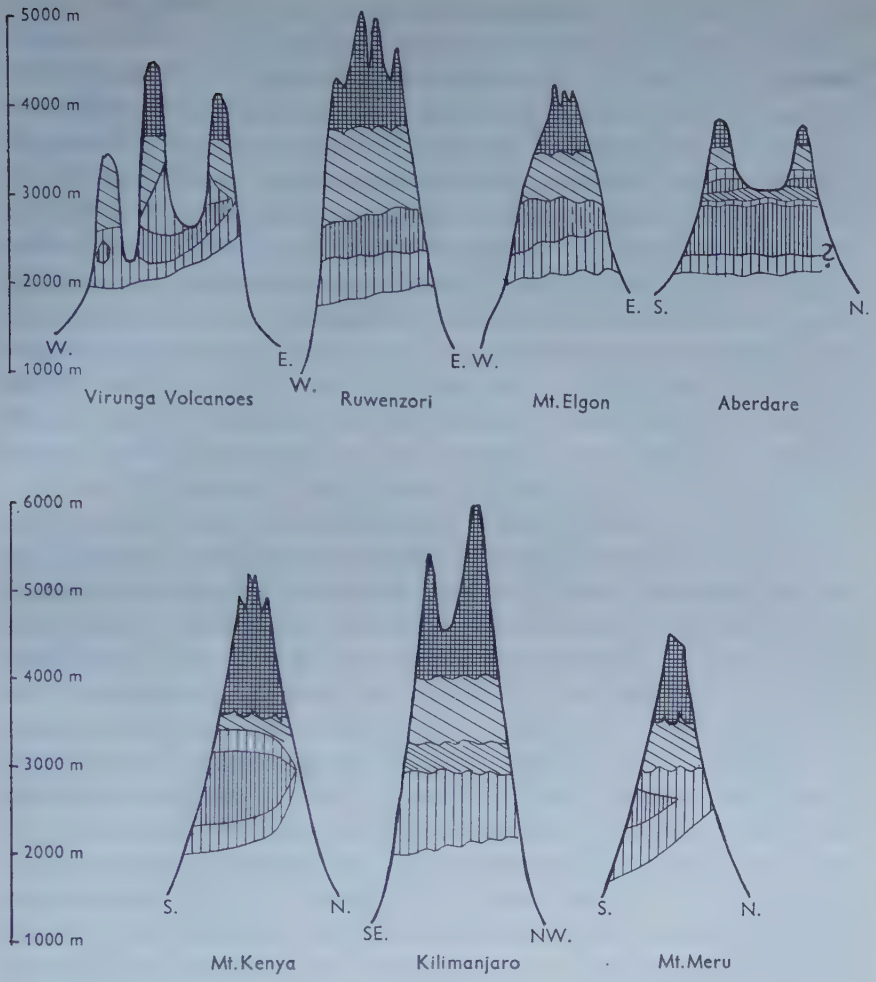

Fig. 4. Schematic profiles showing the vegetation belts of the mountains investigated. The wettest side of each mountain is turned to the left; the letters at their lower parts denote the quarters (W—E; S—N etc.). Where the Montane Forest Belt is differentiated into distinct zones (cp. p. 169) this is indicated by separate marking for the Bamboo Zone. The zone next below is then a Montane Rain-forest Zone, the one next above a *Hagenia-Hypericum* Zone (cp. p. 178 regarding Mt. Meru, however). Only the vertical distances are drawn to scale. — Orig.

tion of the zones he called »subalpine», we get for Ninagongo: 2900—3000 m, Ruwenzori: 3600—4500 m, Mt. Kenya: 3500 à 3600—4790 m, Kilimanjaro: 2600 à 2800—3400 à 3600 m, Mt. Meru: 3000—3600 m; i. e., the upper limits of the »subalpine» zones fluctuate between 3000 and 4790 m. These differences are clearly due to the fact that Giant *Senecios* need much moisture and therefore can ascend high on the wetter mountains, as Ruwenzori and Mt. Kenya, where they get suitable conditions almost everywhere up to their thermal distribution limits. On the higher parts of Kilimanjaro and Meru, however, they are confined to edaphically favoured places, as stream-valleys and small mires, which are very sparse on the higher parts. The »subalpine» and »alpine» zones thus defined on the different mountains are evidently not homologous. Apparently the »tree limit» or »forest limit» is not suitable for demarcating vegetation belts in East Africa.

In spite of the difficulties to distinguish an upper »forest limit» on the East African mountains, the position of that limit and the reasons for its behavior on ridges and in valleys have been debated. To simplify that discussion it might be advisable to study the upper limit of the Ericaceous Belt (cp. p. 178 below) instead of the more or less ill-defined forest limit or timber line (cp. above). The former limit usually ascends higher on the ridges than in the valleys, which may probably sometimes be edaphically conditioned, as on Muhavura (cp. p. 180), sometimes caused by temperature inversion in the bottom of broad, U-shaped valleys, where cold air collects, as on Kilimanjaro (cp. p. 186 and Pl. 2 A). In other cases the Ericaceous Belt ascends higher in the valleys, especially where these are narrow and V-shaped and provide moisture and protection against wind, as on Mt. Kenya and Mt. Meru. In most cases, however, it seems difficult or impossible to discern which of the environmental factors is the most important in determining the limit. — Further observations on the limit in question will be given below.

Most botanists seem to agree that only the zone above the natural forest limit or tree limit ought to be called »alpine» (cp. VAN STEENIS 1935 p. 322). From the facts mentioned above, it appears that the word »alpine» is not quite appropriate for the highest vegetation belt in East Africa, where tree *Senecios* occur. On the other hand, it is very tempting to compare the Ericaceous Belt of the East African mountains (cp. below) with the »subalpine zone» described

by VAN STEENIS (1935) from Malesia, according to him »often consisting of *Ericaceae* for the most part» (*op. c.*, p. 329), and apparently situated at the same level. And then the belt above must correspond to his »alpine» zone. Besides, it is not always easy to distinguish between forest and scrub, i. e., between trees and shrubs. The difference sometimes appears to be mainly due to edaphic factors. — It is not easy to get a better name for the highest belt, either. One possibility would be to adopt the epithet »afro-alpine», which has been used earlier chiefly to denote the »afro-alpine flora element», etc. But against that name the same objections may be raised as against »alpine». And then the latter name is shorter and simpler to use. — The name »*Senecio*-belt» or »*Senecio-Lobelia*-belt» might also be used (cp. MILDBRAED 1914, CHAPIN 1923, GYLDENSTOLPE 1924, ENGLER 1925), but actually the Giant *Senecios* and *Lobelias* are equally common in the upper part of the Ericaceous Belt, and besides they are not very significant for the highest belt on Kilimanjaro and Meru. — A third possible name is *Helichrysum-Alchemilla*-belt (J. W. EGGELING, *in litt.*). These two genera on most of the mountains form a considerable part of the vegetation in the highest belt. But on some mountains one or both of them are rather more important in the Ericaceous Belt, which makes the name a little ambiguous.

Actually, the zone above the Ericaceous Belt is so different on different mountains, that it is very difficult to get a suitable floristic name for it covering all the mountains. Thus I think it is best to keep the old and well-known term »alpine» for the topmost belt. But then the term must be qualified as follows: The Alpine Belt is the zone situated above the Ericaceous Belt, i. e., above the upper limit of more or less continuous Ericaceous (tree- or shrub-)vegetation (cp. Pl. I A, II A). »Alpine» has in fact been used in the above sense by a number of authors dealing with African mountain flora, e. g. COTTON (1932), DUMMER (1919), GRANVIK (1923), HAUMAN (1933, etc.), HUMBERT (1931), JEANNEL (1950), LEBRUN (1935), MILDBRAED (1914), ROBYNS (1937, 1948 etc.) and SNOWDEN (1933). It appears that on the wettest mountains where the Ericaceous Belt is usually developed as forest, most authors have used the same delimitation of the Alpine Zones as adopted here. On the drier mountains, where the Ericaceous Belt is largely developed as scrub, many scientists have, however, not kept that zone apart from

the Alpine Zone as defined above, e. g., ENGLER (1925: Kilimanjaro), R. E. FRIES and TH. C. E. FRIES (1948 and earlier papers), GARDNER (in RENDLE 1932), HANCOCK and SOUNDY (1931), LUGARD (1934), MEYER (1909), MOREAU (1936), SCHIMPER (1935: Kilimanjaro), and SJÖSTEDT (1910).

In the synonym lists below only those names which were apparently intended to cover the zone in question on all East African mountains are quoted as synonyms to the belt names; the other names are enumerated below for each mountain separately. The synonym lists are not claimed to be complete.

2. Montane Forest Belt. General Description.

Synonyms: »Die montane Region» (SCHIMPER 1898); »Subtropische Höhenwaldregion» (ENGLER 1910); »Temperate Rain Forest» (SHANTZ and MARBUT 1923); »Mountain Forest» (CHIPP, in TANSLEY and CHIPP 1926; EDWARDS 1940); »Sub-tropical Evergreen Forest» (PHILLIPS 1930 a); »The East African Mountain Forest Formation» (SNOWDEN 1933); »Montane Rain-forest» (BURTT-DAVY 1935); »Zone des forêts» (JEANNEL 1950). — The »Mountain Forest» of BATTISCOMBE 1936 and »Tropical Upper-montane Rain-forest» of BURTT-DAVY 1938 seem to correspond to the zone called here Montane Rain-forest Zone (cp. below).

The Montane Forest Belt usually extends between 1700—2300 m and 3000—3300 m (cp. Fig. 4). It is distinguished by the occurrence of a great number of broad-leaved hardwood trees and some conifers. Some of the most important species are *Juniperus procera* HOCHST., *Podocarpus gracilior* PILGER, *P. milanjianus* RENDLE, *Olea chrysophylla* LAM., *O. Hochstetteri* BAKER, *Pygaeum africanum* HK. F., *Ekebergia Rueppelliana* A. RICH., *Trichilia Volkensii* GURKE, *Hagenia abyssinica* J. F. GMEL., and *Arundinaria alpina* K. SCHUM. The composition of the forest varies considerably with rainfall and other factors and may be quite diverse on different sides of the same mountain at corresponding altitude (cp. e. g. DALE 1940, EDWARDS 1940). — The lower part of the Montane Forest Belt mostly consists of broad-leaved evergreen hardwoods and some conifers. The leaves of the trees are smaller than in the Lowland Rain-forest, and the epiphytic vascular plants are few, whereas epiphytic mosses and lichens are very important. In the middle part of the belt the bamboo *(Arundinaria alpina)* often attains dominance, and in the highest part of it *Hagenia abyssinica* and *Hypericum leucoptychodes* STEUD. *ex* A. RICH. are often the most important trees (cp. GOOD 1927

regarding the latter name). Thus on some of the mountains, notably Mt. Kenya, the belt contains three distinct zones, namely (from the bottom):

a) Montane Rain-forest Zone.
b) Bamboo Zone.
c) *Hagenia-Hypericum* Zone.

On other mountains the last-mentioned zone is absent, as on Ruwenzori and Elgon, whereas both Bamboo- and *Hagenia-Hypericum* zones are lacking on Kilimanjaro and on the N. part of Mt. Meru. On the W. slopes of Meru, *Hagenia* seems to be the dominant forest tree throughout the belt. — The bamboo is considered by some authors to form only a special (transitional) phase of the montane forest, due to considerable fluctuations because of its peculiar life-cycle (cp. e. g. MILDBRAED 1914 p. 660; HUMBERT 1931 p. 212). On Aberdare the Bamboo- and *Hagenia-Hypericum* Zones are more or less intermingled (cp. p. 183 below). — The three zones mentioned here were described by TH. C. E. FRIES 1923 (FRIES and FRIES 1948) from Mt. Kenya and Aberdare; apparently the same division was proposed by JEANNEL (1950), intended to cover most of the mountains. — In describing the NE. part of the Virunga Volcanoes SNOWDEN (1933) divides the Montane Forest Belt into »(1) a lower Subtropical Zone», apparently corresponding to the Montane Rain-forest Zone, and »(2) an upper Temperate Zone», matching the Bamboo Zone + the *Hagenia-Hypericum* Zone. LEBRUN (1942 p. 80) does not seem to consider the »forêt-prairie à *Hagenia*» to form a separate zone on Ninagongo (and the other Virunga Volcanoes). — We thus find, that whereas the Montane Forest Belt recurs on all the mountains, there is not the same degree of parallelism as to its subdivisions. And so it seems best to keep these zones together, as has been done earlier by a number of authors, e. g. BURTT-DAVY (1935), CHAPIN (1923), EDWARDS (1940), ENGLER (1925: Ruwenzori and Meru), GRANVIK (1923), HUMBERT (1931), JEANNEL (1942, 1950), LUGARD (1934), MILDBRAED (1914), SNOWDEN (1933), and STUHLMANN (1894). — Of course the »Montane Rain-forest Zone» does not entirely consist of rain-forest; also drier forest types occur. On some of the mountains rain-forest prevails in this zone on the wettest side and »Upland Dry Evergreen Forest» on the drier side; sometimes there is a gap in the forest zone on the driest part (cp. below p. 175, 177).

Another zonal division of the Montane Forest Belt was suggested

by BURTT-DAVY (1935 p. 194), comprising also three zones: (1) The Broad-leaf Zone, (2) The Conifer Zone, (3) The Bamboo Zone. — The first two of those zones are hardly altitudinally distinct, however. The main factor controlling the distribution of these two forest types seems to be the amount of precipitation and not altitude (cp. GARDNER 1926 and GARDNER in RENDLE 1932 p. 135; DALE 1940, map). Another important factor, at least for the distribution of »Cedar» *(Juniperus procera)* forest, is fire (cp. WIMBUSH 1937). — LEBRUN (1935 p. 21) subdivided the Montane Rain-forest Zone into three »horizons».

A. Virunga Volcanoes.

The vegetation of these mountains has been studied by a number of botanists, among which may be mentioned MILDBRAED (1914), R. E. FRIES (1920, 1921), HUMBERT (1931, 1934), SNOWDEN (1933), LEBRUN (1935, 1942), and ROBYNS (1937, 1948 a, 1948 b). — Owing to recent volcanic activity in this district (cp. p. 143 above) the vegetation of the lava streams etc. on some of the mountains is far from its »climax» and we find a number of successional types (cp. esp. LEBRUN 1942, ROBYNS 1948 a). Besides, the original forest vegetation has in many places been destroyed by man and replaced by cultivations and diverse types of secondary vegetation (cp. e. g. LEBRUN 1935 p. 13, 26). In this paper only the more or less stable vegetation will be treated; for further particulars the reader is referred to the papers just mentioned, which, i. a., contain extensive bibliographies.

Montane Forest Belt.

Synonyms: »Baumbuschwald (Urbuschwald)» (MILDBRAED 1914: Ninagongo); »Montaner Wald» (R. E. FRIES 1921); »Étage forestier de haute montagne» (HUMBERT 1931); »East African Mountain Forest Formation» (SNOWDEN 1933).

At least on some of these mountains three different zones occur, as described above (cp. Fig. 4).

a. *Montane Rain-forest Zone.*

Synonyms: »Forest Zone» (GYLDENSTOLPE 1924); »Subtropical Zone of the East African Mountain Forest Formation» (SNOWDEN 1933); »Forêt équatoriale de montagne» (SCAËTTA 1934); »Forêt mésophile de montagne» (LEBRUN 1935); »Étage des forêts de montagne» (ROBYNS 1937, 1948 a); »Étage de la forêt ombrophile de montagne» (LEBRUN 1942).

According to Robyns (1948 a) this zone extends approximately between 1750 and 2500 m in the Virunga Volcanoes. Its local extension on the different mountains is rather diverse, however, owing to differences in climate and soil, and to human influence. Thus on the N. slope of the Eastern group of volcanoes (cp. p. 143 above) it has largely been destroyed by man, leaving only a narrow zone of mesophilous forest between c. 2550 and 2650 m (Snowden 1933; author's observations). On the E. slope of Muhavura there appears to be no forest but only short grass and in places low bush (Synge 1937 p. 95; »*British Museum Expedition*»). — On the S. slope of Karissimbi in the Central group the forest extends acc. to Scaëtta (1934) between 1300 and 2300—2400 m. Also on Mikeno and Karissimbi the forest has largely been destroyed by cultivation, however; on some slopes all forest up to the lower limit of the Bamboo Zone at about 2200 m has been eliminated (Lebrun 1935 p. 31). On Ninagongo a Montane Rain-forest Zone is developed between c. 2200 —2500 m (Lebrun 1942).

b. *Bamboo Zone.*

Synonyms: »Bambuswald» (Mildbraed 1914, Engler 1925); »Bamboo Forest» (Gyldenstolpe 1924); »Forêt de Bambous» (Humbert 1931); »Étage à Bambous» (Scaëtta 1934); »Étage des Bambous» (Lebrun 1935, 1942; Robyns 1937, 1948 a); »Upland Bamboo» (Eggeling and Dale 1947). — The Bamboo Zone was further included in: »Temperate Zone of the E. African Mountain Forest Formation» (Snowden 1933).

According to Robyns (1948 a, with map) the Bamboo Zone usually extends from 2300 to 2600 m, reaching up to 3000 m on the Central group of Volcanoes (cp. Scaëtta 1934). No such zone occurs on the E. part of Muhavura (cp. Mildbraed 1914 p. 648), and on the W. group of volcanoes there is only a fragment of bamboo forest on the S. side of Ninagongo (Lebrun 1942). On the NW. slope of Muhavura the present author found the Bamboo Zone to occur between 2650 and 3000 m. Here the bamboo was rather low, in the upper part only 3—4 m high, whereas on the Central group it is reported to attain 20 m in height (Lebrun 1935 p. 14).

c. *Hagenia — Hypericum Zone.*

Synonyms: »Oberer *Hagenia*-Wald» (Mildbraed 1914); »*Hagenia* Zone» (Gyldenstolpe 1924); »*Hagenia*-Formation» (Engler 1925); »Étage à *Hagenia abyssinica* et *Hypericum*» (Scaëtta 1934); »Étage des *Hagenia*»

(Lebrun 1935, Robyns 1937, 1948 a); »Forêt - prairie à *Hagenia*» (Lebrun 1942, Robyns *op. c.*). — Included in »Temperate Zone of the E. African Mountain Forest Formation» (Snowden 1933).

This zone seems to be very well developed on the Central group, where it is reported to occur mainly between 2600 and 3100 m (Robyns 1948 a, with map). For Karissimbi Mildbraed (1914) gives the zone limits 3000—3300 m and Scaëtta (1934) 3000—3500 m. — On the Western group it only occurs in some small fragments (Lebrun 1942 p. 47). In the Eastern group the present author found a rather discontinuous *Hagenia-Hypericum* Zone between about 2900 and 3300 m on the NW. slope of Muhavura. — The vegetation of the zone is usually an open forest formed by 10—12 m high, thick-stemmed trees of *Hagenia abyssinica* and smaller trees or shrubs of *Hypericum leucoptychodes* with an undergrowth of tall herbs, above all *Anthriscus silvestris* (L.) Hoffm.

B. Ruwenzori.

Contributions to our knowledge of the vegetation of this huge mountain have come from a considerable number of scientists, e. g., Stuhlmann (1894), Johnston (1902), Woosnam (1907), Mildbraed (1914), Chapin (1923), Engler (1925), Good (1928), Humbert (1931), Hauman (1933, etc.), Fishlock and Hancock (1933), Lebrun (1935), Synge (1937), and Robyns (1937, 1948 a).

Montane Forest Belt.

Synonyms: »Höhenwald» (Mildbraed 1914, Engler 1925); »Subtropical or Mountain Forest Zone» (Chapin 1923); »Étage forestier de haute montagne» (Humbert 1931); »Lower Forest and Bracken Zones» (Fishlock and Hancock 1933).

a. *Montane Rain-forest Zone.*

Synonyms: »Forest Zone» (Woosnam 1907); »Mountain Forest» (Chapin 1923); »Unterer Höhenwald» (Engler 1925); »Forêt équatoriale de montagne» (Scaëtta 1934); »Forêt mésophile de montagne» (Lebrun 1935); »Mixed Evergreen Rain Forest» (Synge 1937); »Étage des forêts de montagne» (Robyns 1937, 1948 a).

This zone extends between c. 1800 and 2300 m on the W. slopes (Robyns 1948 a; acc. to Scaëtta 1934: 1600—2200 m), 1800 and 2300 m (6000 and 7500 ft.) to the south (Nyamgasani valley, Synge 1937), and between 2050 and 2400 m to the east (Mobuku valley,

author's observations). The lower part of the forest has in many places been destroyed by man, and large areas are occupied by cultivations and secondary vegetation (LEBRUN 1935 p. 30). Where it is left intact it forms a fine rain-forest with tree ferns and wild bananas (*Musa ensete* GMEL.), etc. To the NW., the Montane Rain-forest Zone comes in direct contact with the Lowland Rain-forest (»Forêt ombrophile équatoriale», cp. LEBRUN 1935 Pl. I, ROBYNS 1948 a).

b. *Bamboo Zone* (WOOSNAM 1907; CHAPIN 1923).

Synonyms: »Bambusregion» (MILDBRAED 1914); »Oberer Höhenwald (mit den Bambusbeständen)» (ENGLER 1925); »Forêt de Bambous» (HUMBERT 1931); »Étage à Bambous et à *Podocarpus*» (SCAËTTA 1934); »Étage des Bambous» (LEBRUN 1935; ROBYNS 1937, 1948 a); »Bamboo Forest» (SYNGE 1937); »Upland Bamboo» (EGGELING and DALE 1947).

The altitudinal range of the Bamboo Zone appears to be 2300—2600 m to the west (ROBYNS 1948 a; according to SCAËTTA 1934 it ascends to 2700 or 2800 m) and 2300—3000 m (7500—10,000 ft.) in the Nyamgasani valley to the south (SYNGE 1937). In Mobuku valley to the east the present author found it to be about 2400—3000 m, though the zone is here rather discontinuous.

c. *Hagenia — Hypericum Zone.*

No such zone seems to be present on Ruwenzori though both *Hagenia abyssinica* and *Hypericum leucoptychodes* occur in the upper part of the preceding zone and in the lower part of the Ericaceous Belt (cp. SCAËTTA 1934 p. 303, ROBYNS 1948 a).

C. Mt. Elgon.

Mt. Elgon has perhaps not attracted botanists as much as the preceding two mountain districts. Contributions regarding its vegetation have been delivered by, i. a., JOHNSTON (1902), DUMMER (1919), MILDBRAED (1922), GRANVIK (1923), ENGLER (1925), HANCOCK and SOUNDY (1931), COTTON (1932), LUGARD (1934), SYNGE (1937), DALE (1940), and JEANNEL (1950).

Montane Forest Belt.

Synonyms: »Dense Forests» (GRANVIK 1923); »Forest» (COTTON 1932); »Mountain Forest Zone» (LUGARD 1934).

a. *Montane Rain-forest Zone.*

Synonyms: Part of »East African Highlands» (Dummer 1919); »Unterer Regenwald» (Engler 1925); »Upper Montane Forest» + »High Montane Conifer Forest» (Dale 1940).

The lower limit of this zone lies nowadays at about 2150—2300 m to the east (Lugard 1934; author's observations), and seems to be at about the same level on the other sides of the mountain, though the zone is said to be better developed to the west (Synge 1937). The limit must have been pushed upwards a good deal quite recently by human action (Dale 1940 p. 75). The upper limit of the zone against the Bamboo Zone fluctuates between 2400 and 2650 m, being highest to the east (Dale *op. c.*). The different forest types and their distribution on Mt. Elgon have been described and mapped by Dale *(op. c.)*.

b. *Bamboo Zone* (Dummer 1919).

Synonyms: »Bambusregion» (Engler 1925); »Montane Bamboo Forest» (Dale 1940); »Upland Bamboo» (Eggeling and Dale 1947).

The Bamboo Zone forms a ring round Mt. Elgon, except for a small gap to the north (Dale *op. c.*, p. 77). The bamboo appears to be better developed on the W. side, where it occurs between 2400 and 3000 m (Dale *l. c.*), than to the east (cp. Synge 1937), where it only begins at about 2650 m and forms a rather discontinuous zone up to c. 2850 m, though single patches of bamboo have been observed as high as 3350 m (author's obs.).

c. *Hagenia — Hypericum Zone.*

No distinct such zone has been reported from Mt. Elgon, though isolated groves of *Hagenia* trees occur from 2600 up to 3300 m.

D. Aberdare, and E. Mt. Kenya.

The flora and vegetation of these mountains have been thoroughly studied by R. E. Fries and Th. C. E. Fries (cp. Th. C. E. Fries 1923, R. E. Fries 1925, Fries and Fries 1948, extensive bibliography in the latter work). Further contributions are due, i. a., to Engler (1925), Rendle (1932), Moreau (1945; with bibliography), and Jeannel (1950). — The lower vegetation-zones of the two mountains are fairly similar, as demonstrated by the Fries brothers, and accordingly they may be treated together.

Montane Forest Belt.

Synonyms: »Zone forestière» (Alluaud et Jeannel 1914); »Zone des forêts» (Jeannel 1942).

a. *Montane Rain-forest Zone.*

Synonyms: »Montaner Regenwald» (Th. C. E. Fries 1923, Engler 1925); »Forest Belt» (Rendle 1932); »Mountain Forest» (Chapin 1933); »Mountain Rain-forest Zone» (Fries and Fries 1948).

This zone forms on Mt. Kenya a huge crescent, leaving an open gap to the north (cp. Rendle 1932, Synge 1937 p. 108). Its vertical distribution appears to be between 2000—2200 and 2400 m on the W. slopes of Mt. Kenya (Fries and Fries 1948) and 2400—2700 m towards NE. (Jeannel 1950 p. 113). On Aberdare the limits are according to Fries and Fries (*op. c.*, p. 8) about the same; the present author found the figures to be 2200—2400 m on the central E. slope of the mountain. Also on Aberdare there seems to be a gap in the Montane Forest Belt to the north (cp. »Map of Central Kenya in 1 : 1 000 000», publ. by the Government Printer, Nairobi, 1948). These circumstances need further study, however. — Two types of »Mountain Rain-forest» were described by Fries and Fries *(op. c.)*, called »Drier Rain Forest» and »Humid Rain Forest». The former type would, however, hardly be classified as rain-forest by English foresters but rather as »Tropical High-montane Conifer-forest» (Burtt-Davy 1938) or »Upland Dry Evergreen Forest» (Eggeling and Dale 1947).

b. *Bamboo Zone* (Fries and Fries 1948).

Synonyms: »Bambusregion» (Th. C. E. Fries 1923, Engler 1925); »Zone of Pure Bamboo (*Arundinaria alpina*)» (Rendle 1932); »Bamboos» (Chapin 1933); »Niveau de Bambous» (Jeannel 1942); »Bamboo Belt» (Moreau 1945).

The Bamboo Zone extends between about 2400 and 3200 m on the W. slopes of Mt. Kenya (Fries and Fries 1948, author's observations), 2500 and 3200 m towards NW., and between 2700 and 3000 m towards NE. (Jeannel 1950). On the E. slope of Aberdare it ranges between 2400 and 3000 m (author's obs.), and on the W. side between 2700 and 3200 m (Jeannel *op. c.*). On the latter mountain it also forms separate zones between about 3100 and 3300 m

on Kinangop and Sattima (Fries and Fries *op. c.*, author's obs.; cp. p. 183 below). On both mountains the Bamboo Zone appears to be continuous in its lower part, except for a gap to the north. — Fries and Fries (*op. c.* and earlier papers) subdivided the zone into one Lower and one Upper Bamboo Zone.

c. *Hagenia — Hypericum Zone* (Fries and Fries 1948).

Synonyms: »*Hagenia* - *Hypericum lanceolatum* - Region» (Th. C. E. Fries 1923), »Höhenwald» (Engler 1925); »*Hagenia* Woods» (Chapin 1933).

This zone occurs between 3200 and 3450 m on Mt. Kenya (W. slopes) and between 3050 and 3400 m (discontinuous) on Aberdare (author's observations). On the high plateau of Aberdare there is a peculiar intermingling of Bamboo, *Hagenia-Hypericum*-vegetation, and »moorlands», which will be discussed later in connection with the Ericaceous Belt (p. 183).

F. Kilimanjaro.

Of the East African high mountains, Kilimanjaro is perhaps the one which was best explored in the early days (cp. p. 154 above), notably by Johnston (1886), Meyer (1890, 1900, 1909), Volkens (1897), and Sjöstedt (1910). Important vegetational notes have further been published by Tobler —Wolff und Tobler (1914), Gillman (1923), Engler (1925), Cotton (1930), and Moreau (1936). A historical account of its botanical exploration is found in Cotton *(op. c.)*.

Montane Forest Belt.

Synonyms: »Urwald» (Meyer 1890); »Gürtelwald» (Volkens 1897, Engler 1925); »Montane Region» (Schimper 1898, 1935); »Urwaldzone» (Meyer 1900, Tobler-Wolff und Tobler 1914); »Nebel- oder Höhenwald (temperierter Hochgebirgsregenwald)» (Meyer 1909); »Regenwald oder Gürtelwald» (Sjöstedt 1910); »Forest Zone» (Gillman 1923); »Highland Forest» (Moreau 1936); »Zone des forêts» (Jeannel 1942).

On Kilimanjaro the Montane Forest Belt is less differentiated than on the other mountains, neither Bamboo nor *Hagenia-Hypericum* Zones occur. The belt was divided by Engler (1925) into two parts: »Unterer Höhenwald bis zum Beginn der *Podocarpus*» and »Oberer Höhenwald». It extends on the S. slope between c. 1900 and

2600—3000 m (ENGLER *op. c.*) or 3100 m (S. of Kibo, VOLKENS 1897 p. 162); to the SE. (above Marangu) the present author found its range to be c. 1950—2950 m. To the north, where it occurs from 2200—2800 m (ENGLER *l. c.*) it seems to be of a drier type with still less differentiation (»Was auf der Südseite zonenweise getrennt ist, wächst hier in mannigfacher Mischung neben- und durcheinander» — MEYER 1900 p. 121). — Throughout the Montane Forest Belt there seems to have been a good deal of human influence (cutting and burning) and a considerable part of the ground is occupied by secondary vegetation, as *Eupteris, Philippia*-forest, etc.

Below the Montane Forest Belt there are zones of »mixed forest» and cultivation, which have been treated by, i. a., VOLKENS (1897), MEYER (1900, 1909), and ENGLER (1925).

G. Mt. Meru.

Regarding the vegetation of Mt. Meru little has been published. The most important sources are UHLIG (1904), JAEGER (1906), MEYER (1909), SJÖSTEDT (1910), ENGLER (1925), and MOREAU (1936).

Montane Forest Belt.

Synonyms: »Regenwaldgürtel (SO-Seite)» (JAEGER 1906); »Höhenwald (auf der Südost- und Südseite)» (ENGLER 1925). — (These names apparently comprise also the fragments of »Lowland Rain-forest» on the SE slope).

On the moist S. slopes this belt is developed between c. 1700 and 2700 m (5700 and 9000 ft., MOREAU 1936) and contains two distinct zones (Montane Rain-forest Zone and Bamboo Zone). On the other (drier) parts of the mountain there is not such a clear differentiation; to the E., where the ground largely consists of more or less fresh lava streams (cp. p. 156 above), the belt is represented by »High-mountain Scrub» (»Hochgebirgsbusch») between 2100 and 2700 m (UHLIG 1904, ENGLER 1925), and on the W. slope the present author found *Hagenia abyssinica* to be the dominant forest tree throughout the belt, which extends from about 2550 to 3050 m. The undergrowth here mainly consists of *Stoebe kilimandscharica* O. HOFFM. To the N. there is said to be a gap in the forest belt (cp. UHLIG *op. c.*, MOREAU *op. c.*), which would certainly merit further investigations. — The lower edge of the forest has, to the south at least, recently been pushed back by man (cp. MOREAU *op. c.*, p. 857).

a. *Montane Rain-forest Zone.*

Synonyms: »Regenwald» (Uhlig 1904, Meyer 1909, Sjöstedt 1910); »Höhenwald, untere Stufe» (Engler 1925); »Highland Forest» (Moreau 1936). — The first synonym apparently comprises also the fragments of Lowland Rain-forest on the SE. slope.

This zone only occurs on the SE. part of Mt. Meru, extending between about 1700 and 2300 m (5700 and 7500 ft., Moreau *op. c.*).

b. *Bamboo Zone.*

Synonyms: »Bambuszone» (Uhlig 1904); »Bambus-Dickicht» (Meyer 1909); »Bambuzone» (Sjöstedt 1910); »Höhenwald, mittlere Stufe (Bambuszone)» (Engler 1925); »Belt of Bamboos» (Moreau 1936).

Also the Bamboo Zone is confined to the S. slopes, extending here between c. 2300 and 2700 m (7500 and 9000 ft., Moreau *op. c.*).

c. *Hagenia — Hypericum Zone.*

No distinct such zone is known from Meru, though the zone called by Engler (*op. c.*, p. 268) »Höhenwald, obere Stufe» (2700—2900 m on the S. slopes; with *Hagenia abyssinica* etc.) might be something like it. Engler's description was, however, made chiefly after notes on Uhlig's plant collections only, and further field studies are required.

3. Ericaceous Belt. General Description.

Synonyms: »Subalpine Zone», of »The East African Mountain Subalpine and Alpine Formation» (Snowden 1933); »Heathland type of vegetation» (Burtt-Davy 1935); »Zone subalpin» (Jeannel 1950). — The belt has further been included in: »Alpine Region» (Schimper 1898); »Subalpine und alpine Region» (Engler 1910); »Alpine Meadow» (Shantz and Marbut 1923); »Alpine Zone» (Phillips 1931); »Tropical Alpine Elfin-Woodland» (Burtt-Davy 1938); »Mountain Grassland or Heathland» (Edwards 1940). On my herbarium labels the name »*Philippia*-region» has sometimes been used.

The vegetation of the Ericaceous Belt is usually dominated by arborescent or shrubby species of *Philippia*, the commonest being *Philippia excelsa* Alm *et* Th. Fr. jr. In the lower part of the belt the genus *Erica* often plays an important rôle (*Erica arborea* L. and other species), and here will also occur some broad-leaved trees as

Rapanea sp. and *Hypericum leucoptychodes* Steud. *ex* A. Rich., etc. The lower limit of the belt lies at about 2600—3400 m, and the upper limit fluctuates between 3550 and 4100 m (cp. Fig. 4). — As will be seen from the account below, the appearance of the belt is quite different on different mountains. Sometimes it is represented by a dense *Erica-Philippia*-forest, sometimes by an open scrub of the same genera. The homology between the Ericaceous Zones of the different mountains seems to be indisputable, however. Thus the forest and scrub are formed by the same or closely related species of *Philippia* and *Erica*, and there is on the whole considerable floristic agreement. The big physiognomic differences are apparently largely due to climatic and edaphic divergences between the mountains. Another important factor in this connection is fire, generally caused by man. Whereas the climate of the Ericaceous Belt on most mountains is usually rather wet during most of the year, we do get dry seasons, and then the tree- or shrub-heathers are easily set on fire. And as it is an age-old practice in Africa to set fire to the grass and scrub during the dry season (cp. e. g. Phillips 1930 a, b), it is no wonder that fires will sometimes occur in this belt on most of the mountains. They may in fact constitute one of the main reasons why the belt on some of the mountains is developed as low *Philippia* scrub or as moorland with scattered trees and shrubs only, and not as forest. The evidence at hand of the influence of fire will be surveyed below for each mountain separately. — Fires on the upper part of high mountains are known also from other places in the tropics, as Mt. Cameroon (cp. Mildbraed 1914 p. 667) and in New Guinea (Lane-Poole 1925 p. 65 etc.).

In former days all of the arborescent *Ericoideae* of the higher parts of the East African mountains used to be called *Ericinella Mannii* or *Erica arborea*. On closer study of this group Alm and Fries (1927 a, b) distinguished a number of closely related species, which were mainly arranged in the genera *Philippia* and *Erica*. As these species — and even the genera — are very difficult to distinguish when not in flower, our knowledge of their relative frequencies on most of the mountains is still rather incomplete. When, for instance, some author has reported *Erica arborea* L. to be the dominant species on a certain slope, it may mean only that he found one flowering specimen of the said species among a number of sterile ones, which looked very much the same but might easily have been some species of *Philippia* instead. On some mountains *Erica*

seems to be the most important genus in the lower part of the belt and *Philippia* the most important higher up. For these reasons, it would not be advisable to use any of these generic names alone in the denomination of the belt.

As before, the appearance of the belt will be described for each of the mountains separately.

A. Virunga Volcanoes. Pl. III A, IV B.

Synonyms: »Formation der *Ericacéen* oder subalpiner Sträucher (*Ericacéen*formation)» (Mildbraed 1914); »Subalpine Region» + »Alpine Region» (R. E. Fries 1921: Ninagongo; Engler 1925: Ninagongo); »Tree Heath Belt» (Gyldenstolpe 1924); »Peuplement de Bruyères arborescentes» (Humbert 1931); »Subalpine Zone» (Snowden 1933); »Étage à Bruyères arborescentes» (Scaëtta 1934); »Étage des *Ericacées*» (Lebrun 1935); »Étage des Bruyères arborescentes (étage subalpin)» (Robyns 1937, 1948 a); »Étage subalpin à *Ericacées*» (Lebrun 1942).

The vertical extension of the belt is about 2700—3470 m (summit) on Ninagongo in the W. group of volcanoes (Lebrun 1942), 3500—3800 m on the S. slope of Karissimbi (Scaëtta 1934), 2600—3700 m on the Central group in general (Robyns 1948 a), and 3000—3600 m (10,000—12,000 ft.) on the E. group (Snowden 1933). On the NW. side of Muhavura the present author found the limits to be c. 3200—3700 m (cp. map in Robyns *op. c.*). — The pronounced relief of the young volcanoes with radiating sharp ridges, separated by deep and narrow valleys, causes a marked edaphical and microclimatical diversity. The ridges are in this belt usually occupied by *Erica arborea* L. and *Philippia Johnstonii* (Schw.) Engl., often overloaded with *Usnea* lichens (cp. Pl. III A, IV B), whereas the most prominent species of the valleys are often *Senecio Erici-Rosenii* R. E. Fr. *et* Th. Fr. jr. and *Hypericum leucoptychodes*. — The »*Ericetum*» of the ridges may sometimes be rather dry; one night during my stay there (at about 3400 m on the W. slope of Muhavura) my porters were a little careless with fire and before we could do anything about it most of the camp was burned, together with some hundred square metres of »*Ericetum*».

B. Ruwenzori. Pl. I A, I B.

Synonyms: »Hochmoor mit *Erica*-Wald» (Stuhlmann 1894); »Tree-heath Zone» (Woosnam 1907, Chapin 1923); »*Ericacéen*-region (subalpin)» (Mildbraed 1914); »Subalpine *Ericacéen*region mit moosigem Niederwuchs (W-

Seite)», and »Subalpine Buschregion mit moosigem Niederwuchs (O-Seite)» (ENGLER 1925); »Peuplement de Bruyères arborescentes» (HUMBERT 1931); »Étage subalpin (*Ericetum*)» (HAUMAN 1933, etc.); »Étage à Bruyères arborescentes et *Rapanea pellucido-striata* GILG *et* SCHELL.» (SCAËTTA 1934); »Étage des *Ericacées*» (LEBRUN 1935); »Heather Forest Zone (*Ericetum*)» (SYNGE 1937); »Étage des Bruyères arborescentes» (ROBYNS 1948 a).

On Ruwenzori the Ericaceous Belt forms a wide girdle round the mountain (cp. map in ROBYNS 1948 a), extending between c. 3000 and 3900 m (10,000 and 13,000 ft.) in the Nyamgasani valley to the S. (SYNGE *op. c.*), 2700—3800 m to the W. (HAUMAN 1933), and 2900—3800 m to the E. (author's observations). — At the upper border of the belt the *Ericetum* usually keeps to the slopes, leaving the valley bottoms open (cp. Pl. I A). — The belt was subdivided by HAUMAN on the W. slope into two zones, called: »*Ericetum* riche en espèces» (2800—3300 m) and »*Ericetum* pauvre en espèces» (3300—3800 m) (*op. c.*, p. 911). Another subdivision was proposed by SYNGE (*op. c.*, p. 199) in the Nyamgasani valley.

The main tree growth in the lower part of the belt seems to be formed by *Erica arborea* L., *E. Bequaertii* DE WILLD, and *Philippia Johnstonii* ENGL., intermingled with some *Podocarpus* or broad-leaved trees as *Hypericum spp.*, *Rapanea sp.*, and *Hagenia abyssinica* J. F. GMEL. In the higher part the most important rôle is played by *Philippia Johnstonii* and *Ph. longifolia* ENGL. together with *Senecio Erici-Rosenii* R. E. FR. *et* TH. FR. JR. (ROBYNS *op. c.*; cp. Pl. I B). — One of the most conspicuous features of the Ericaceous Belt of Ruwenzori lies in the ground cover, which consists of thick, swelling carpets of mosses and liverworts, the most important species being *Breutelia Stuhlmannii* BROTH., *Sphagnum spp.*, *Plagiochila ericicola* STEPH., etc. (cp. HAUMAN *op. c.*). Not only the ground but also the tree trunks and branches are covered by foot-deep moss-cushions. These seem to be almost permanently soaked with water (cp. p. 149 above), thus, e. g., making it possible for *Scirpus fluitans* L. to occur as a terrestrial plant in the ground cover of closed forest. All patches of level ground seem to be occupied by *Carex runssoroensis*-bogs. — Nevertheless dry spells may occur at certain periods, at least in the upper part of the belt; during such a period SYNGE and his companions, camping in the upper part of Nyamgasani valley, had their camp burned down together with the surrounding vegetation (SYNGE *op. c.*, p. 44). — A burned forest area in the lower part of this belt was reported by STUHLMANN (1894 p. 289).

C. Mt. Elgon.

Synonyms: »Heath Zone» (Dummer 1919, Dale 1940); »Transition Belt to *Erica* Zone» + »*Erica* Zone» (Granvik 1923); »Subalpine Grasslands with Scattered Ericaceous Bushes and Suffruticose Plants of Temperate Genera» (Cotton 1932); »Prairie subalpine» (Jeannel 1950). — The Ericaceous Belt of Elgon was further included in: »Subalpine und alpine Region» (Engler 1925); »Alpine Zone» (Hancock and Soundy 1931, Lugard 1934).

The Ericaceous Belt of Mount Elgon, which extends between c. 3000 and 3550 m (Granvik 1923, Cotton 1932, author's observations), is very different from that of Ruwenzori. The definition by Cotton quoted above gives rather a good picture of it; a considerable part of the belt consists of grassland with scattered trees or shrubs of *Philippia excelsa* Alm *et* Th. Fr. jr., *Erica arborea* L., and the ericoid *Compositae, Stoebe kilimandscharica* O. Hoffm., the latter perhaps being the commonest one of the three. Between these grasslands occur patches of forest, where may occur, besides the species just mentioned, *Hagenia abyssinica* J. F. Gmel., *Senecio amblyophyllus* Cotton, and *S. elgonensis* Th. Fr. jr., etc. In the ground cover, grasses also play the most important rôle in these patches of forest, and mosses are insignificant. — At the upper limit of the zone, the tree heaths seem to avoid the valley bottoms and keep to the middle part of the valley slopes, giving place to strips of »alpine» vegetation along the streams.

The appearance of this belt must largely be due to human influence. Thus, in its lower part are situated a number of small villages, inhabited by »elgonis» (sometimes called »elgon masai»), whose ancestors are said to have long since taken refuge in these altitudes to escape plundering expeditions of warriors from Suk and Karamoja (Lindblom 1921 p. 109). We visited three such villages to the E., two of which were situated at c. 3200 m, and the third one at about 2600 m down in the Montane Forest Belt. These elgonis have rather big herds of cattle, which are kept grazing in the environs, and to improve the grazing they often burn the grass during the dry season. The grasslands in the Ericaceous Belt may therefore be regarded as a high-altitude parallel to the savanna round the foot of the mountain, which also seems to owe its present appearance to grass-fires and grazing (cp. »*Ruwenzori Expedition 1934 -5*» p. 3).

D. Aberdare.

Synonyms: No specific name appears to have been given to this zone on Aberdare before; it was, however, included in the following: »Regio alpina inferior» (Th. C. E. Fries 1923); »Untere subalpine Region» (Engler 1925); »Alpine Moorlands» (Rendle 1932); »Alpine Zone» (Fries and Fries 1948).

As mentioned above the zonation of Aberdare is very complicated. Its vegetation zones may be briefly outlined as follows (cp. Fig. 4): Round the W., S., and E. slopes of the basal range extends the Montane Forest Belt, containing a very substantial Bamboo Zone, which at its upper limit is fringed by a narrow *Hagenia-Hypericum* Zone (cp. p. 176 above). Then comes a big and rather flat high-plateau at about 3000—3300 m, above which rise the two peaks of Kinangop and Sattima. Most of the high-plateau seems to be covered by tussock-grassland, »moorland», with scattered patches of bamboo (usually with a fringe of *Hypericum leucoptychodes* Steud. *ex* A. Rich., etc.) and trees or shrubs of *Hagenia, Hypericum, Stoebe kilimandscharica* O. Hoffm., and *Clifforthia aequatorialis* R. E. Fr. *et* Th. Fr. jr. Above this plateau, on the slopes of Kinangop and Sattima we again encounter local Bamboo and *Hagenia-Hypericum* Zones. Above these comes a narrow Ericaceous-shrub Zone, stretching on Kinangop between c. 3400 and 3675 m. Finally, there is a delimited Alpine Zone, largely consisting of tussock-grassland with certain resemblances to the ground cover of the preceding zone and the moorland lower down.

In their »Alpine Zone» Fries and Fries (1948) united the moorlands with the two highest of the zones just mentioned on Kinangop and Sattima. The appearance of the moorland was attributed by them (*op. c.*, p. 9—10) to climatical phenomena, viz., temperature inversion on the big, partly depressed plateau. Whether climatic or edaphic factors are the most important in this case may be difficult to decide, however. The Bamboo and *Hagenia-Hypericum*-vegetation appears to show some preference for sloping ground, whereas flat areas are more often occupied by »moorland». Biotic factors must not be forgotten, either, notably human influence. Undoubtedly there is a rather lively traffic across the Aberdare Range in east-westerly direction, and grass-fires are probably not rare during the dry season, though I have no direct evidence of this. Grazing may also be of some importance; at least on the S. part of the plateau there is plenty of game, such as elephant and

buffalo. As demonstrated by EGGELING (1947 p. 33) elephants and grass-fires in combination may sometimes not only retard the regeneration of forest once destroyed but even actively diminish the forested area.

When comparing Aberdare with the other mountains one will find, that — both regarding altitudinal extent and general physiognomy — the Moorland Zone corresponds rather closely to the lower part of the Ericaceous Belt on Mt. Elgon and Kilimanjaro (cp. p. 182, 186). The author thus finds it best to unite the Moorland Zone with the Ericaceous-shrub Zone higher up, notwithstanding the fact that they are usually separated by local Bamboo and *Hagenia-Hypericum* Zones. — This classification differs from the one used by FRIES and FRIES *(op. c.)* chiefly in the more restricted meaning of the term »alpine». Accordingly, we get two different zones in the Ericaceous Belt of Aberdare:

1) Moorland Zone.
2) Ericaceous-shrub Zone.

The latter zone has got about the same apearance as the Ericaceous Belt on Mt. Kenya (cp. below).

E. Mt. Kenya.

Synonyms: Same as for Aberdare (p. 183); furthermore included in »Zone des prairies alpins» (ALLUAUD et JEANNEL 1914); »Zone des tussocks alpins» (JEANNEL 1942), and »Moorland» (MOREAU 1945).

On Mt. Kenya the Ericaceous Belt extends between 3400 and 3550 à 3600 m (Teleki valley, author's observations). In its lower part, there occurs a narrow zone of closed *Philippia*-forest with trees up to 6 m tall (cp. MOREAU 1945 p. 63), which is a little broader in sheltered valleys and may be absent on ridges. Higher up only shrubs of *Philippia* and *Erica* occur, between which the ground is largely covered by wet tussock-grassland of about the same type as in the lower part of the Alpine Belt. — Along narrow, sheltered valleys one often finds narrow strips of Ericaceous scrub up to at least 4000 m. These are usually not continuous with the Ericaceous Belt proper, however, and should preferably be classified with the Alpine Belt. They seem to be formed mainly by *Philippia keniensis* S. MOORE. — The lower limit of the belt is a very marked floristical limit; few species occur on both sides of it (cp. FRIES and FRIES 1948 på 72).

The main reason why the upper part of the Ericaceous Belt is

developed as scrub and not as forest seems to be recurrent fires, which are apparently easily initiated during the dry season. Thus MACKINDER (1900 p. 466) describes how a considerable part of the Alpine and Ericaceous Belts were burned off during his visit when a lighted match was dropped on the ground. Also some time shortly before 1920 part of the belt must presumably have been burned, as appears from Plate 38 B and 39 A in R. E. FRIES 1925, where one may see skeletons of dead Ericaceous shrubs. According to SYNGE (1937 p. 111) the mountain plateau to the north had been swept with fire a couple of years before 1935. On my visit in 1948 I found the *Philippia* and *Erica* shrubs to be burned over a considerable area in the upper part of the belt; most of them were regenerating by means of basal shoots, at that time about 0.4 m high. I was told that about 5 years before there had been a big fire. — In this way the upper limit of the Ericaceous Belt may have been depressed; above that limit I found a number of burned *Philippia* specimens which had not recovered.

It is easy to understand why the Ericaceous Belt has not earlier been kept distinct on Mt. Kenya, since as a rule it is poorly developed there. Besides, the Giant *Senecios* and *Lobelias* which occur there are much more conspicuous than the *Philippia* shrubs. But a classification based on these endemic plants is apparently not as useful when comparing the vegetation zones of different mountains.

F. Kilimanjaro.

Synonyms: »Grasfluren» (MEYER 1890); »Subalpine Region» (ENGLER 1925). — The Ericaceous Belt was further included in »Bergwiesen» (VOLKENS 1897, SJÖSTEDT 1910); »Alpine Region» (SCHIMPER 1898, 1935); »Gras- oder Staudenzone» (TOBLER-WOLFF und TOBLER 1914); »Alpine grass and shrub vegetation» (GILLMAN 1923); »Alpine Zone» (MOREAU 1936); »Zone des prairies alpines» (JEANNEL 1942). — For synonyms as to the subdivisions see below.

The Ericaceous Belt of Kilimanjaro contains two different zones, distinguished already by VOLKENS (1897), viz. (1) »Moorland Zone», and (2) »Ericaceous-shrub Zone». — These zones seem to correspond to those described from Aberdare (p. 184).

1. *Moorland Zone.*

Synonyms: »Grasflur-Formation» (VOLKENS 1897); »Grasflurenregion» (MEYER 1900); »Alpine Grasflur» (MEYER 1909); »Grasfluren» (TOBLER-

Wolff und Tobler 1914); »Formation der Bergwiesen» (Engler 1925); »Moorland» (included in »Alpine Zone») (Moreau 1936).

This zone extends on the SE. slopes from c. 2800—2900 m up to about 3250 m (author's observations). On the steeper SW. slopes it seems to be narrower because the Montane Forest Belt ascends here up to 3100 m (Volkens *op. c.*, p. 162), and above Machame the Moorland Zone is stated to be absent, being replaced by tree-heather forest, continuous with the Ericaceous-shrub Zone (Moreau 1936 p. 852). However, the Moorland Zone seems to form a girdle round most of the mountain between about 2800 and 3250—3400 m (cp. Engler 1925). It consists of tussock grassland with scattered low trees or shrubs of *Philippia excelsa* Alm *et* Th. Fr. jr., *Ph. Jaegeri* Engl., and *Erica arborea* L., etc. One of the most conspicuous flowering plants of the zone is *Helichrysum Meyeri-Johannis* Engl. — For further details about this zone see Volkens (*op. c.*, p. 306 ff.); good pictures are to be found in Tobler-Wolff und Tobler (1914 Pl. 14), Moreau (*op. c.*, Pl. III: 1), and Jeannel (1950 Pl. XII).

2. *Ericaceous-shrub Zone.* Pl. II A, II B.

Synonyms: »*Ericinella*-Formation» (Volkens 1897); »Reine *Ericinella*-Formation» (Meyer 1900); lower part of »Alpine Krummholzformation» (Meyer 1909); »*Ericinella*-Region» (Sjöstedt 1910); »Busch- und *Ericinella*-Formation» (Engler 1925).

The dominant shrubs of this zone appear to be the same species as in the Moorland Zone, intermingled with, i. a., *Protea kilimandscharica* Engl., *Adenocarpus Mannii* Hook f., *Anthospermum usambarense* K. Schum., and, on mires and along streams, *Senecio Cottonii* Hutch. *et* Tayl. and *S. Kilimanjari* Mildbr. In the lower part of the zone the shrubs are usually 1—2 m high and stand rather close together, whereas in the upper part they only attain a height of ½ - 1 m and cover only a fraction of the ground, leaving much bare soil between them (cp. Pl. 2 B). — The zone extends from the upper limit of the Moorland Zone at about 3250 m up to 3900 m (Engler 1925) or 4000 m (Meyer 1900); on the SE. slope the present author found it ascending to about 4100 m. The upper border is rather sharp and easily seen from a long distance; it is situated considerably higher on the ridges than in the broad valleys (Pl. 2 A).

The present appearance of the Ericaceous Belt must largely be attributed to fire, caused by man. Within memory, the upper parts

of the mountain have often been visited by the Africans (cp. e. g. JOHNSTON 1886), and large fires in this belt have been reported several times. Thus MEYER (1900 p. 127, 182) states that on his visit here vast stretches of »*Ericinella*-Formation» had recently been burned on the NW. and SW. slopes. A little later, UHLIG reports from the SE. slopes (on a herbarium specimen of *Philippia Jaegeri* ENGL.; UHLIG 74, 5.X. 1901, in Amani Herbarium): »In dieser Gegend über Moschi alles verbrannt, die Reste 2 m hoch, daneben ½ m hohe selten blühende Schiesslinge . . .» — MEYER (1890 p. 114) considered that the upper limit of the Montane Forest Belt had been pushed down by grass-fires occurring in the Moorland Zone above.

G. Mt. Meru.

Synonyms: »Buschwald von Baumerika» (JAEGER 1906); »*Ericinella*-Formation» (MEYER 1909); »Ericinellen» (included in »Alpine Region»; SJÖSTEDT 1910); »Subalpine Region (Formation der *Erica arborea*, Bergwiesen)» (ENGLER 1925). — The belt was further included in the »Alpine Region» of MOREAU (1936).

The vertical extension of the Ericaceous Belt seems to be about 3000—3600 m to the S. (ENGLER 1925) and 3050—3450 m to the W., though in one ravine a lobe of it ascends as high as 3650 m (author's observations). In the saddle between Meru and its satellite to the N., Longorno, the upper limit of the belt reaches 3700 m. — The lower parts are developed as a more or less closed *Philippia*-forest. In the higher parts the trees are often dwarfed and shrubby, and the *Ericetum* is dissolved into lobes, separated by stretches of loose, dry sand with sparse vegetation. On wet places in the lower part of the belt occurs *Senecio meruensis* (COTTON and BLAKELOCK 1948).

Also on Mt. Meru there is evidence of devastating fires in the Ericaceous Belt. A few weeks before my visit to the mountain, in October 1948, there had been a big fire on the N. slope, and a broad fire-break had been cut across the forest of the W. slope. On Longorno to the north, the *Ericetum* had been largely burned down.

4. Alpine Belt. General Description.

Synonyms (cp. p. 167): »Alpine Zone» of »The East African Mountain Subalpine and Alpine Formation» (SNOWDEN 1933); »The Zone of Tree Groundsels and *Lobelias*» (BURTT-DAVY 1935); »Zone alpine» (JEANNEL 1950). — The belt was further included in: »Alpine Region» (SCHIMPER

1898); »Subalpine und alpine Region» (ENGLER 1910); »Alpine Meadow» (SHANTZ and MARBUT 1923); »Alpine Zone» (PHILLIPS 1931); »Tropical Alpine Elfin-Woodland» (BURTT-DAVY 1938); »Mountain Grassland or Heathland» (EDWARDS 1940).

Owing to climatic and other differences, the Alpine Belt is rather diverse on the different mountains, and it is not easy to give any common vegetational characteristics, except the position above the border of the Ericaceous Belt. On corresponding altitudes, the vegetation varies from dense and moist forests of Giant *Senecios* on Ruwenzori to open, desert-like grass-communities on Mt. Meru. The most important genera of vascular plants of the Alpine Belt are *Senecio, Lobelia, Alchemilla,* and *Helichrysum,* the first two containing those well-known giant types, and the last two represented chiefly by shrubby species. In this belt also occur a number of genera of boreal affinity, as *Agrostis, Anthoxanthum, Arabis, Cardamine, Cerastium, Deschampsia, Festuca, Poa, Ranunculus,* and *Sagina,* which also occur in the Ericaceous Belt and a little lower down but are absent in the lowlands of Tropical Africa (cp. e. g. ENGLER 1910 p. 989). — We may also distinguish a number of plant communities that are more or less typical of this belt (cp. HAUMAN 1933, FRIES and FRIES 1948). The most important are: (1) *Senecio*-forest, predominated by arborescent *Senecios,* different species on each mountain; (2) *Helichrysum*-scrub, which may sometimes be dense and more than 2 m high, as on Ruwenzori, sometimes open and only half a metre high or less, as on Kilimanjaro, and which is also largely dominated by different species on different mountains; (3) »*Alchemilletum*»-communities, formed by shrubby *Alchemillas* of different species; (4) *Carex*-bogs, with tall tussocks of *Carex runssoroensis* K. SCHUM. or related species; (5) Tussock-grassland (moorland).

The climate of the Alpine Belt of equatorial mountains is of a very peculiar type, described by TROLL (1943, 1948) as »Frostwechsel-Klima». It is characterized by changes from frost to thaw and the reverse almost every day of the year, which causes frost-lifting and solifluction. In connection with this some very remarkable life-forms of plants occur here.

The flora of the Alpine Belt was the main object of my field work in Africa, and special studies were devoted i. a. to the composition of the main plant communities and the life-forms of the alpine plants. Time and space do not permit a discussion of these ques-

tions here, however. The author will confine himself to a brief sketch of the appearance of the belt in each of the mountain districts investigated.

A. Virunga Volcanoes.

Synonyms: »*Senecio*formation» (Mildbraed 1914); »*Senecio* Belt (*Senecio* and *Lobelia* Zone)» (Gyldenstolpe 1924); »Étage alpin» (Humbert 1931, Lebrun 1935, Robyns 1937, 1948 a); »Alpine Zone» (Snowden 1933); »Étage subalpin à *Lobelia* et Seneçons arborescentes» + »Étage alpin» (Scaëtta 1934).

The Alpine Belt extends on the higher mountains from 3600—3700 m to the summit (Robyns 1948 a, author's observations). The volcanoes of the W. group are apparently not high enough to have an alpine zone (Lebrun 1942). — The main plant communities of the belt are *Alchemilletum,* often predominated by *Alchemilla geranioides* Rolfe, and *Senecio*-forests, formed in the main by *Senecio alticola* Mildbr., *S. refractisquamatus* De Willd., and *S. Erici-Rosenii* R. E. Fr. *et* Th. Fr. jr. In some places occur also *Carex runssoroensis*-bogs and *Helichrysum*-scrub (cp. Burtt 1934, Robyns 1948 a). According to Burtt (*op. c.,* p. 165) who visited all the main peaks of this group, their flora is essentially the same.

B. Ruwenzori. Pl. IV A, V A.

Synonyms: »*Lobelia* and Groundsel Zone» + »Snow Zone» (Woosnam 1907); »*Senecio*-Region (»alpine» Region)» (Mildbraed 1914); »*Senecio* - *Lobelia* (alpine) Zone» + »Snow» (Chapin 1923); »Subalpine *Senecio*- und *Lobelia*-Region» + »Alpine Region» (E. slope) and »Subalpine *Senecio*-Region» (W. slope) (Engler 1925); »Highest floral zone» (Good 1928, Fishlock and Hancock 1933); »Étage alpin» (Humbert 1931, Hauman 1933, Lebrun 1935, Robyns 1937, 1948 a); »Étage subalpin et alpin à *Lobelia* et *Senecio* arborescents» (Scaëtta 1934).

On Ruwenzori the Alpine Belt extends from about 3800 m to the summits. Its vegetation on the W. side of the mountain has been thoroughly studied by Hauman (1933), and his description seems to hold good also for the S. parts (Synge 1937) and for the E. slope of the mountain (author's observations). The four most important plant communities distinguished by Hauman are: *Senecio*-forest, *Helichrysum*-scrub, *Alchemilletum,* and *Carex runssoroensis*-bog (cp. Pl. V A).

Senecio-forests occur chiefly on rather steep ground with plenty

of mobile ground-water and some shelter against wind exposure, as in small side-valleys etc. (cp. Pl. IV A, V A), their main distribution being between 3800 and 4300 m to the W. (Hauman *op. c.*) and 4000 – 4350 m to the E. (author's observations). They are often very dense and form a biocoenose with a local climate of its own. The most wide-spread and important of the alpine plant communities is perhaps the *Helichrysum*-scrub, predominated by *Helichrysum Stuhlmannii* O. Hoffm., which seems to prefer less steep slopes and more shallow soil, and seems to endure more wind exposure than the *Senecio*-forest. The scrub is usually 1—2 m high and very thick, being difficult to pass without cutting a path. The valley bottoms are often flat (cp. p. 147) and occupied (as in the Ericaceous Belt) by *Carex runssoroensis*-bogs, distinguished by densely spaced tussocks of *Carex runssoroensis* K. Schum. in a *Sphagnum*-carpet, together with some scattered Giant *Senecios* etc. On more or less gentle and well-drained slopes, as moraine-ridges etc., the vegetation usually consists of *Alchemilletum*, predominated by *Alchemilla geranioides* Rolfe, *A. argyrophylloides* Bak. f. etc. (Pl. V A). — For further details regarding these plant communities see Hauman *op. c.* and de Grunne *et al.* 1937. Their distribution on an ordinary mountain slope is beautifully illustrated in a sketch on p. 605 in the first-mentioned paper.

C. Mt. Elgon. Pl. V B.

Synonyms: »Alpine zone of the crater and peak» (Dummer 1919); »Alpine Region» (Granvik 1923); »True Alpine Zone» (Cotton 1933); »Upper moorlands» (included in »Alpine Elfin Woodland»; Dale 1940). — The Alpine Belt of Elgon was further included in: »Subalpine und alpine Region» (Engler 1925); »Alpine Zone» (Hancock and Soundy 1931, Lugard 1934).

The Alpine Belt extends from about 3550 m to the summits, including all of the huge »crater» and a wide zone along its outside. In its vegetation, *Senecio*-forests (chiefly composed of *Senecio Gardneri* Cotton at higher levels and *S. elgonensis* Th. Fr. jr. in the lower parts) play an important rôle (cp. Pl. V B), though they are not so dense as on Ruwenzori. They seem to be confined to localities with plenty of ground water in motion, as on steep slopes and along small rills, etc. — On rocky ground with thin soil the vegetation often consists of open and low *Helichrysum*-scrub, and on gently sloping ground in the crater *Alchemilletum* is important. On flat and badly drained ground there occur a number of tussocky

Carex-bogs (Pl. V B). — The most important plant community of the belt, however, seems to be tussock-grassland (moorland), covering probably more than half of its area. The large extension of the latter community may partly be due to fire. As mentioned before, there is a native track across the »crater» (cp. p. 150), and the Africans passing here often start grass-fires. Thus in May 1948 the present author saw wide areas of grassland NW. of »Maji ya moto» that had recently been burned, and according to HANCOCK and SOUNDY (1931 p. 173) the grass is in places burned every year (cp. also p. 182 above). These fires evidently give the grassland advantage over the *Alchemilletum*, which seems to be more slow-growing.

D. Aberdare.

Synonyms: There does not seem to exist any direct synonym to the Alpine Belt on Aberdare as here delimited; the belt was included in: »Regio alpina» (TH. C. E. FRIES 1923); »Obere subalpine Region» (ENGLER 1925); and »Alpine Zone» (FRIES and FRIES 1948).

On Aberdare the Alpine Belt comprises only two small caps on the highest parts of Kinangop and Sattima, from about 3675 m to the summits at 3906 and 3875 m, respectively (cp. p. 183 above and Fig. 4). At least on Kinangop most of the belt seems to be occupied by moorland; Giant *Senecios* occur (*S. aberdaricus* R. E. FR. *et* TH. FR. JR.), but are hardly forest-forming, and *Alchemilletum* chiefly occurs in the Ericaceous Belt. — Of the plant communities described from the higher parts of Aberdare by FRIES and FRIES (1948) only the »*Koeleria convoluta* - *Alchemilla cyclophylla* - Association» and the »*Senecio aberdaricus* - Association» seem to occur in the Alpine Belt acc. to the present definition.

E. Mt. Kenya. Pl. III B.

Synonyms: No exact synonym seems to have been published; however, the Alpine Belt as defined here seems to correspond to: most of »Zone des prairies alpines», + »Désert alpin» (ALLUAUD et JEANNEL 1914); most of »Regio alpina», + »Nivale Region» (TH. C. E. FRIES 1923); most of »Subalpine Region», — »Alpine (nivale) Region» (ENGLER 1925); most of »Zone des tussocks alpins», + »Désert alpin» (JEANNEL 1942); most of »Alpine Zone», + »Nivale Zone» (FRIES and FRIES 1948). — The belt was further included in »Alpine Moorlands» (GARDNER in RENDLE 1932 p. 135), and »Moorland» (MOREAU 1945).

In the Alpine Belt of Mt. Kenya, which extends from about 3600 m to the summit, three different zones were distinguished by TH. C. E.

FRIES (1923), which were named in FRIES and FRIES 1948: (1) the »Lower Alpine Zone» up to 3860 m, containing much *Senecio Brassica* R. E. FR. *et* TH. FR. JR. but no *S. keniodendron* R. E. FR. *et* TH. FR. JR.; (2) the »Upper Alpine Zone» up to 4500 m, distinguished by presence of *Senecio keniodendron,* whereas *S. Brassica* is almost absent. In (3) the »Nivale Zone», finally, no Giant *Senecios* occur, and only scattered specimens of a few hardy flowering plants are present, together with mosses and lichens. Although the limits between these zones are not very sharp (there is, e. g., considerable overlapping of the ranges for *Senecio Brassica* and *S. keniodendron*), such a division seems to be useful on Mt. Kenya. The border between the first two zones should probably be placed at about 4000 m. — It must be remembered, however, that the »Lower Alpine Zone» of FRIES and FRIES comprises also the Ericaceous Belt of the present classification.

In the »Lower Alpine Zone» the vegetation consists chiefly of moorland (tussock-grassland) with scattered specimens of *Senecio Brassica* (Pl. III B). This community, which has been described by FRIES and FRIES (1948 p. 46: »The *Senecio Brassica* - *Festuca* Association»), also occurs in the upper part of the Ericaceous Belt (cp. p. 184). — In the »Upper Alpine Zone» occur some patches of *Senecio keniodendron*-forest, which seems to be confined to localities with good supply of (mobile) ground water (cp. FRIES and FRIES 1948 p. 47). The undergrowth is mostly predominated by shrubby *Alchemillas,* sometimes by *Festuca*-tussocks (cp. FRIES and FRIES *l. c.*). Solitary specimens of *Senecio keniodendron* also occur in other plant communities. — *Alchemilletum* often occurs without tree *Senecios* and is one of the most important communities of this zone; it seems to prefer sloping ground, probably with some moving subsoil water. — On flat and moist ground in valley bottoms occurs a *Lobelia keniensis* - *Agrostis* - community, whereas on well-drained to dry slopes the main vegetation is a type of tussock-grassland, predominated by *Festuca Pilgeri* ST.-Y and *F. abyssinica* HOCHST. *ex* A. RICH. — The above description holds good for the W. slopes; towards N. and NE. the »Lower Alpine Zone» seems to be much drier (cp. JEANNEL 1950 p. 113).

That grassland of different types plays such an important rôle in the Alpine Belt of Mt. Kenya may perhaps partly be due to influence by fire (cp. p. 179, 185).

F. Kilimanjaro. Pl. VI A, VI B.

Synonyms: »Alpine Zone» (Engler 1925). — The Alpine Belt as defined above further corresponds to: »Staudenregion» + »Steinflechtenregion» (Meyer 1890); upper part of »Bergwiesen», + »Flechtenregion» (Volkens 1897); upper part of »Alpine Krummholzformation», + »Alpine Wüste» (Meyer 1909); upper part of »Bergwiesen (alpine Gras- und Staudenzone)», + »Gipfel (hochalpine Zone)» (Sjöstedt 1910); upper part of »Gras- oder Staudenzone», + »Gipfel» (Tobler-Wolff und Tobler 1914); upper part of »Alpine grass and shrub vegetation», + »Alpine desert» (Gillman 1923); upper part of »Alpine Zone» (Moreau 1936); upper part of »Zone des prairies alpines», + »Désert alpin» (Jeannel 1942).

The Alpine Belt extends on Kilimanjaro from c. 4100 m upwards. In its lower part up to c. 4300 m a *Helichrysum*-community dominates, composed mainly by *Helichrysum Newii* Oliv. *et* Hiern, *H. Hoehnelii* Schweinf., and *H. fruticosum* (Forsk.) Vatke (cp. Pl. VI B). Another important shrub of this belt is *Euryops dacrydioides* Oliv. (cp. Pl. VI A). — Tree *Senecios (S. Cottonii* Hutch. *et* Tayl.) occur sparsely in the lower part of the belt in edaphically favoured places with sufficient ground water (cp. Gillman 1923 p. 10), though their main distribution appears to be in the Ericaceous Belt (cp. p. 186). — The ground of this zone seems to be still drier than in the upper part of the Ericaceous Belt; the vegetation covers less than half of the surface. Solifluction terraces and polygones are common, as in the upper part of the next lower belt.

Higher up the vegetation gets still scantier, with stray grass-tussocks of the genera *Festuca, Agrostis, Pentaschistis* and *Koeleria*, together with some odd specimens of *Helichrysum, Senecio, Carduus*, etc. (Pl. VI A). — The larger part of the saddle between Kibo and Mawenzi (cp. p. 154) was denoted by Meyer (1900, 1909) as »Alpine Desert» (»alpine Wüste»). Vegetation of vascular plants is absent or very sparse, except for some places, where subsoil water appears (cp. p. 156 above), and where we accordingly get patches of more or less closed vegetation. One such locality was observed on the W. slope of Mawenzi at about 4550—4800 m (cp. Meyer 1900 p. 150); another one in the S. central part of the saddle at c. 4400 m. For further notes on the alpine vegetation se Volkens 1897 (p. 315 ff.) and Meyer 1900.

G. Mt. Meru.

Synonyms: »Hochwüste» (Uhlig 1904); upper part of »Alpine Region» (Sjöstedt 1910); »Alpine Region» (Engler 1925); upper part of »Alpine Zone» (Moreau 1936).

Most of the Alpine Belt of Mt. Meru consists of a dry scree, harbouring an open steppe-like community, predominated by two grasses of the genus *Pentaschistis*, and containing 6 species in all. At rock precipices and other edaphically aberrant places a few more species occur, but the alpine flora seems to be extremely poor. This must largely be due to dryness (cp. p. 157). — These observations were made on the W. and NW. slopes, but according to Uhlig (1904) conditions seem to be more or less the same to the south.

The highest parts of the crater rim are rocky and a little less dry; about 10 species of flowering plants were found right up to the summit at c. 4560 m.

Conclusion.

When comparing the vegetation of the different high mountains in East Africa, one is struck as much by their dissimilarities as by their similarities (cp. Fig. 4). The basic factor, causing altitudinal differentiation, is of course altitude, manifested in the first place in decreasing temperatures towards higher levels, and further in changes in air pressure, radiation climate, etc., all of which have their bearing on the vegetation. This complex of factors must, together with the more or less common »biota», be mainly responsible for the similarities found in vegetation zonation between the mountains. — On these factors are superimposed, however, a number of other factors of more local development, e. g., amount of precipitation, frequency of clouds and mist, inclination of the ground, chemical and physical properties of bed-rock and soil (e. g. water-holding capacity), biotic influences (e. g. agriculture, grazing, fire), etc. These factors, together with differences between the »biotas» of different mountains, constitute the main reasons for the differences between them as to vegetation zonation. To establish in detail the rôle played by each factor will be a very difficult task, requiring more extensive knowledge of all the factors mentioned. Such studies may, however, be of some importance in connection with forest conservation.

When studying the Montane Forest Belt we often find larger differences between different sides of the same mountain than between different mountains. The two highest belts seem to be more uniform on each mountain, however, and if we keep to them the mountains may be arranged in a series according to increasing

»dryness» (as manifested in the vegetation). That series would be: Ruwenzori, Virunga Volcanoes, Mt. Kenya, Aberdare, Elgon, Kilimanjaro, and Mt. Meru (cp. JEANNEL 1950 p. 198). — The effects of human influence on the upper parts seem to be most important on the last five.

In conclusion it may be well to point out once more, that when the name »alpine» is used here for the topmost belt of vegetation, that does n o t mean that the author considers that belt to be directly homologous with the Alpine Belt of Europe. In fact such a comparison is hardly possible, since both climate and flora are entirely different (cp. TROLL 1948). It would be easier to make a comparison between the vegetation zones of East Africa and Malesia, though we had perhaps better wait for a detailed comparison before stating any homologies.

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Plate I.

A. Ruwenzori: Bujuku valley from the lower part of Mijusi valley (c. 3700 m). Ericaceous Belt. The dark patches are *Philippia* forest, keeping at its upper limit to the valley slopes (cp. p. 181). In the foreground Giant *Senecios* and *Helichrysum Stuhlmannii*. Note the man near the lower left corner. — Photo A. Holm 26.3. 1948.

B. Ruwenzori: Bujuku valley near Bigo camp, c. 3400 m. Ericaceous Belt. Small glade in *Philippia* forest (trees 7—8 m tall) along a stream. In the foreground *Senecio Erici-Rosenii* (right) and semi-arboreal *Peucedanum Kerstenii* (left). — Photo Å. Holm, March 1948.

Plate II.

A. Kilimanjaro, part of the SE. slope above Peter's Hut (c. 3800 m). Ericaceous Belt. The dark vegetation covering most of the central part in the picture is Ericaceous scrub (cp. the lower picture). The light patch in the centre is a mire. The upper limit of the Ericaceous Belt is clearly visible, being lower in the broad valley than on the adjoining ridges (cp. p. 186). In the background appear the rugged peaks of Mawenzi. — Photo Å. Holm, June 1948.

B. Kilimanjaro, SE. slope near Peter's Hut, c. 3800 m. Ericaceous Belt. Ericaceous scrub; the shrubs are usually 0.5—1 m tall. Between them there is much bare soil and scattered specimens of *Helichrysum* and *Blaeria* etc. — Photo O. Hedberg 15.6. 1948.

Plate III.

A. Muhavura, W. slope, c. 3700 m. *Philippia*-shrubs at the upper limit of the Ericaceous Belt, about 2—3 m tall and with their stems entirely covered by *Usnea* lichens. The vegetation in the foreground is *Alchemilletum* (cp. p. 189); in the centre and back appear some Giant *Senecios*. — Photo O. Hedberg, October 1948.

B. Mount Kenya, W. slopes, c. 3700 m. Alpine Belt. Moorland in the Lower Alpine Zone, with scattered specimens of *Senecio Brassica* (leaf rosettes), and *Lobelia keniensis* (small columns). — Photo O. Hedberg 25.7. 1948.

Plate IV.

A. Ruwenzori, Bujuku Valley near Lake Bujuku, c. 4000 m. Alpine Belt. *Senecio*-forest with *Lobelia Wollastonii* etc. Note the dead old inflorescences on the *Senecios* and the climbing *Rubia* cfr. *ruwenzoriensis* on the stems in the centre. — Photo O. Hedberg, March 1948.

B. Muhavura, E. slope, c. 3500 m. Ericaceous Belt. Dense and low *Philippia* forest on a dry ridge in the upper part of the belt; the stems are hidden by *Usnea* lichens. — Photo O. Hedberg 6.10. 1948.

Plate V.

A. Ruwenzori, in a side valley to the west from Bukurungu valley, c. 4000 m. Alpine Belt. The light patch in the centre is a *Sphagnum* bog, surrounded by *Carex runssoroensis* - tussocks. In the lower left corner and in the centre behind the bog *Alchemilletum* prevails; upper left corner: *Senecio* forest. — Photo O. Hedberg 4.4. 1948.

B. Mount Elgon, in the SW. part of the »crater», c. 3900 m. Alpine Belt. The flat space in the centre is a mire with *Carex*-tussocks, whereas the surrounding slopes are covered by *Alchemilletum* with scattered trees of *Senecio Gardneri*, in the background forming an open forest (cp. p. 190). — Photo O. Hedberg 14.5. 1948.

Plate VI.

A. Kilimanjaro, in the S. part of the saddle, c. 4400 m. Alpine Belt. Open, steppe-like *Festuca*-community. The dark shrubs in the background are *Euryops dacrydioides;* in the lower left corner two rosettes of *Carduus sp.* Note the frost-lifting structure of the soil surface (cp. p. 193). — Photo O. Hedberg 15.6. 1948.

B. Kilimanjaro, SE. slope above Peter's Hut, c. 4200 m. Alpine Belt. *Helichrysum-Festuca*-community in the lower part of the belt, with much bare soil. — Photo O. Hedberg 15.6. 1948.

A

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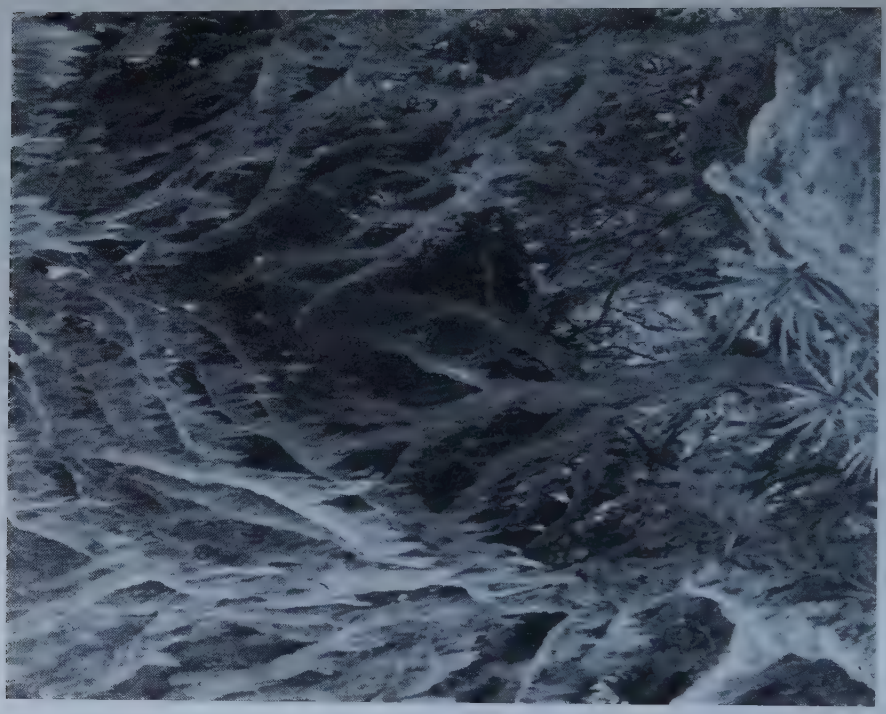

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Svensk Botanisk Tidskrift. Bd 45, H. 1. 1951.

EINIGE NEUE OPHIOSTOMA-ARTEN IN SCHWEDEN.

VON

AINO MATHIESEN.

Während der letzten Jahre wurde an der Forstlichen Versuchsanstalt Schwedens das Verhältnis zwischen den gewöhnlichsten nadelholzbewohnenden Borkenkäfern und den durch sie verbreiteten Bläuepilzen studiert. Material aus verschiedenen Gegenden Schwedens wurde durchgearbeitet (Rennerfelt 1950). Dabei stellte es sich heraus, dass gewisse Borkenkäfer konstant von Bläuepilzen begleitet werden und andere nicht. Die Assoziation zwischen den Borkenkäfern und Bläuepilzen ist sehr spezialisiert, indem gewisse Käferarten konstant von einer bestimmten, für sie spezifischen Pilzart begleitet werden. Die Pilze sind von den Käfern hauptsächlich verbreitungsbiologisch abhängig. Zum gleichen Resultate sind vorher z. B. Rumbold (1931, 1936), Grosmann (1930), Leach (1940) u. a. gekommen, im Gegensatz zu Webb (1946), der hauptsächlich einen Pilz, *Leptographium Lundbergii* Lag., den er biologisch zu den Ambrosiapilzen stellt, als die einzige wichtige Borkenkäferbegleitende Bläue auffasst und ihm mit den meisten untersuchten Borkenkäferarten assoziiert findet. — Weiter stellte es sich heraus, dass in Schweden, wie in anderen Ländern, die meisten der mit den Borkenkäfern assoziierten Bläuepilze zu der Gattung *Ophiostoma* gehören, und dass hier teils dieselben Pilze, welche schon aus den Nachbarländern als wichtige Bläueerreger bekannt sind, eine wichtige Rolle spielen, wie z. B. *Ophiostoma penicillatum* (Grosm.) Siem. auf der Fichte; teils aber eigene, bisher wenig bekannte oder unbeschriebene Arten, wie z. B. *O. canum* (Münch) Nannf. und *O. clavatum* n. sp. auf der Kiefer, von grosser Bedeutung sind.

Näheres über die gewöhnlichsten Bläuepilze Schwedens und ihre Beziehungen zu den Wirtkäfern findet man in den früheren Arbeiten von Rennerfelt (1950) und Mathiesen (1950). Unter den untersuchten Arten befanden sich einige, die zum erstenmal in Schweden angetroffen wurden, und einige, die bisher unbeschrieben waren. Eine Beschreibung der neuen und der bisher in der Literatur wenig bekannten Arten, deren Originalbeschreibung wenigstens in Schweden schwer zugänglich ist, wird in dieser Arbeit gegeben. Die Kulturen der neubeschriebenen Arten werden in der Forstlichen Versuchsanstalt Schwedens aufbewahrt und auch CBS in Baarn zugesendet. Die Beschreibung der Reinkulturen, wenn nicht anders angegeben, geschieht nach ihrem Wachstum auf 2,5 % Malzagar. Die Zahlen für Zuwachsgeschwindigkeit beziehen sich auf den radialen Zuwachs in cm auf 2,5 % Malzagar bei 22° C nach 10 Tagen (nach Lagerberg 1927).

Die Gattung Ophiostoma Syd.

Eine eingehende historische Übersicht über die Gattungen *Ceratostomella* und *Ophiostoma* wird von Rumbold (1911) und Nannfeldt (1934) gegeben. Die Gattung *Ceratostomella* wurde von Saccardo 1878 aufgestellt. Bei einer Revision dieser Gattung von Winter (1887) wurde der Typus der jetzigen *Ophiostoma, O. piliferum,* zu *Ceratostomella* gestellt. Schon 1918 entdeckte v. Höhnel, dass die Asci der Arten, auf denen Saccardo die Gattung begründete und die von *C. pilifera* verschieden sind, und er stellte für den letzteren Typus die neue Gattung *Linostoma* auf. Da dieser Name nicht benutzt werden konnte, benannten H. & P. Sydow (1919) die Gattung um, zu *Ophiostoma*. Nannfeldt (1932) hat die systematische Stellung der Gattungen *Ophiostoma* und *Ceratostomella* näher untersucht. Die Gattung *Ceratostomella* gehört nach ihm zu den wahren Pyrenomyceten (s. str.), zu *Sphaeriales, Ascohymeniales,* nahe der Gattung *Phomatospora* Sacc. Nach dem Aufbau der Asci gehört *Ophiostoma* zu den Plectascales und steht in der Nähe von *Aspergillus* und *Microascus*. Auch die zytologischen Untersuchungen von Varitchak (1931), Mittman (1932) und später von Andrus & Harter (1933, 1937) haben bestätigt, dass die Entwicklung der Fruchtkörper bei *Ophiostoma*-Arten ähnlich vor sich geht wie bei den Plectascales. Goidànich (1936) gibt folgendes phylogenetisches Schema über die angrenzenden Gattungen: *Penicillium* . .

Aspergillus — Microascus — Grosmannia — Ophiostoma — Ophiostomella — Petriella — Chaetomidium — Chaetomium — Ascotricha.

Trotz der bewiesenen Heterogenität der Gattung *Ceratostomella* werden bis in die letzte Zeit von mehreren Systematikern die *Ophiostoma*-Arten fortgesetzt unter *Ceratostomella* gestellt. Andererseits werden für Arten, die sich nur durch mindere und nicht konstante Eigenschaften der Perithezien unterscheiden, neue Gattungen aufgestellt, hauptsächlich auf Grund der verschiedenen Konidienformen. Zu solchen Gattungen gehören *Endoconidiophora* (Münch 1908) und *Grosmannia* (Goidànich 1936). Die Behauptung, dass selbst die Gattung *Ophiostoma* s. str. einer neuen Revision bedarf (Francke 1950), weil man hier Arten mit prinzipiell abweichendem Ascusbau findet, scheint berechtigt zu sein. Nach den bisherigen Untersuchungen ist aber soviel klar, dass Arten mit schlauchförmigen Asci, zu Ascohymeniales gehörend, und Arten mit rundlichen, irregulär in der Fruchtkörperhöhlung entstehenden Asci zu getrennten Gattungen gestellt werden müssen, und dass für die letzteren Arten von den verschiedenen vorgeschlagenen Namen *Ophiostoma* am meisten berechtigt ist. Die bisher vorgeschlagenen Abtrennungen neuer Gattungen von *Ophiostoma* gründeten sich hauptsächlich auf die Nebenfruchtform und sind nicht genug motiviert. So ist z. B. das im folgenden näher beschriebene *O. polonicum* Siem. ein gutes Biespiel für die Übergangsformen zwischen den Arten der *Grosmannia*-Gruppe und den übrigen *Ophiostoma*-Arten. Sowohl *Endoconidiophora* wie *Grosmannia* sollten als Artgruppen unter *Ophiostoma* gestellt werden.

1. **Ophiostoma minutum** Siem.

(Abb. 1 a—g.)

Fundorte: Ulriksfors (Jmtl.), Hamra (Dlr.), Hofors (Gästrl.), Bogesund (Uppl.), meist auf Kiefer, weniger oft auf Fichte, in alten Frassbildern der Borkenkäfer *Blastophagus minor, Pissodes piniphilus, Ips acuminatus* und *I. typographus*, zusammen mit anderen *Ophiostoma*-Arten.

Ophiostoma minutum ist von Siemaszko (1939) aus Polen als ein zufälliger Begleiter von *Ips typographus* auf Fichten beschrieben worden. Ausserdem ist er von Davidson (1942) in Nord-Amerika zusammen mit *Monochamus titillator* auf totem Kiefernholz gefunden worden.

Dieser Pilz scheint in Schweden auf feucht liegendem berindetem Kiefernholz nicht selten zu sein, aber er wird wegen seiner sehr kleinen, *Ophiostoma pini*-ähnlichen, zerstreut auf der Holzoberfläche und in den Insektgängen stehenden Perithezien oft übersehen.

Die Perithezien auf dem Holze sind dunkelbraun, rundlich, kahl oder mit einzigen kurzen, braunen Haaren, 58—106 μ im Durchmesser (Mittel 67 μ), somit, wie bei DAVIDSON (60—80 μ), etwas kleiner als bei SIEMASZKO, wo 84—140 × 74—125 μ angegeben wird Perithezienhälse sind zylindrisch, 60—100 μ lang (45—90 μ DAVIDS.; 98—140 μ SIEM.), 20 μ breit (14—20 μ SIEM.) und tragen einen kurzen, konischen, hyalinen Zilienkranz mit 8—10 hyalinen, schmalen, zugespitzten Zilien, 7 × 1 μ. Die Asci werden schnell verschleimt. Ascosporen sind lang und schmal, spindelförmig, an beiden Enden lang zugespitzt und etwas gekrümmt, 13,3 × 1,7 μ (8—10 × 1—1,5 μ SIEM.; 10—15 × 1 μ DAVIDS.). Die Sporen werden, eingebettet in Schleim, als lange, fadenschmale, 2—4 μ breite Ranken aus den Perithezien herausgepresst und sammeln sich nicht wie bei anderen *Ophiostoma*-Arten zu einem Schleimklumpen am Perithezienhalse, sondern bleiben als lange Fäden frei in der Luft schweben. Die Ascosporen werden leicht im Wasser dispergiert.

Die Reinkultur von *Ophiostoma minutum* auf Malzagar verläuft folgendermassen. Die Sporen keimen langsam, in 1 % Malzlösung nach za. 48 Stunden. Das Myzelwachstum ist sehr langsam, 0,83 cm. Bei 2—3 Wochen alten Kulturen wird die Wachstumsgeschwindigkeit noch geringer und kann schon vor Erschöpfung des Nährbodens aufhören. Einsporenmyzelien haben eine hemmende Wirkung aufeinander.

Das Substratmyzel ist anfangs hyalin, dann etwas gräulich, aus dichten, sehr schmalen, 1,9—3,2 μ breiten und reichlich verzweigten Hyphen mit zahlreichen Öltropfen bestehend. Das Luftmyzel ist weiss, aus sehr schmalen Hyphen bestehend und wird spärlich gebildet, weshalb die Oberseite der Kolonien leicht seidenglänsend erscheint. Am Luftmyzel werden spärlich Konidien an *Cephalosporium*-artigen Köpfchen gebildet, terminal an Spitzen kurzer Hyphen, welche oft wirtelig an längeren, unbegrenzt wachsenden Hyphen angeordnet sind. Die Myzelkonidien sind einzellig, hyalin, sehr klein, 3—4 × 1,6 μ, elliptisch bis eiförmig. An Substrathyphen werden zahlreiche Konidien gebildet, meist akrogen an kurzen Hyphen. Die Konidien vermehren sich hefeartig und bilden dichte, schleimige Konidienanhäufungen zwischen den Myzelfäden. Das

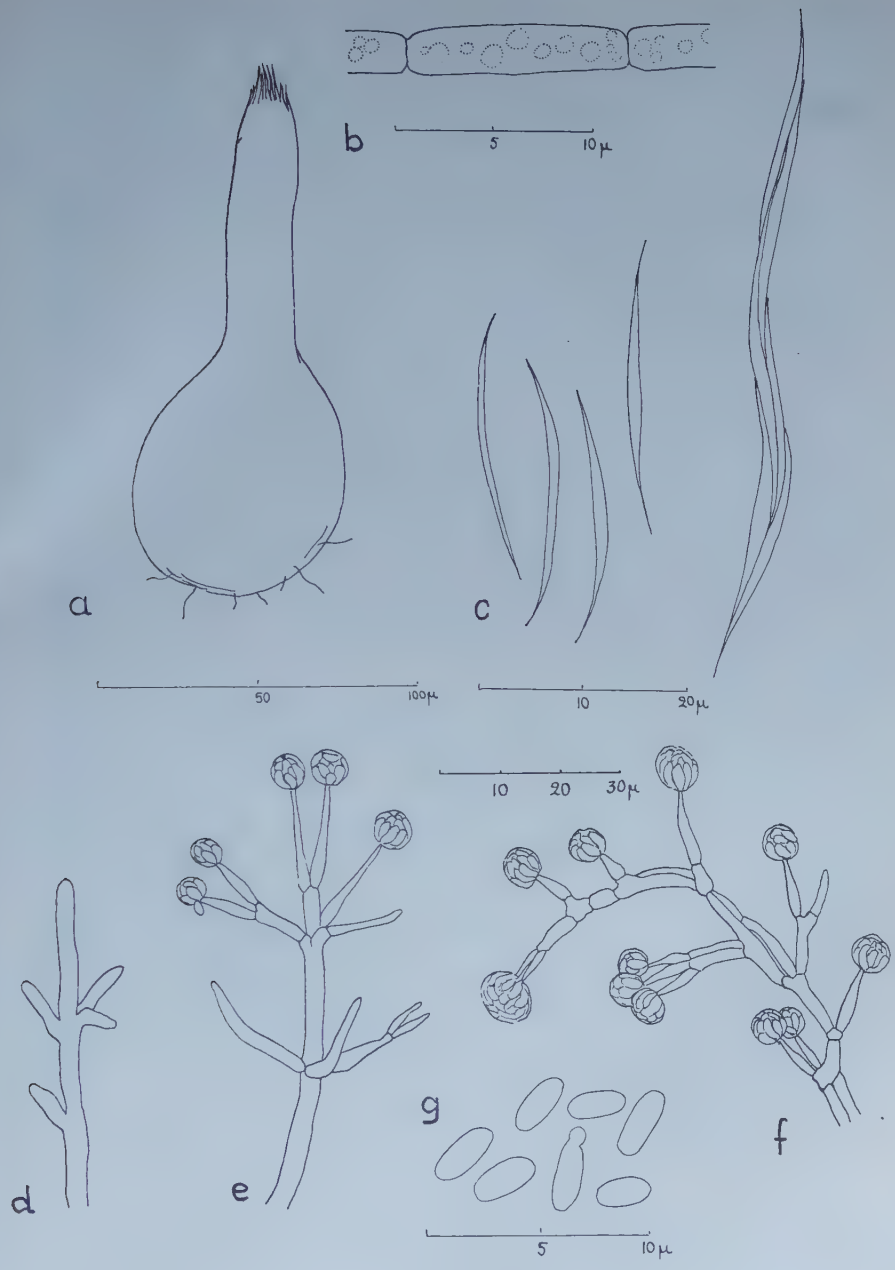

Abb. 1. *Ophiostoma minutum* Siem.: a) Perithezium, b) Substrathyph, c) Ascosporen, d—g) Myzelkonidien und Konidienträger.

Substratmyzel und die Konidien haben eine Neigung, in konzentrischen Zonen gebildet zu werden. Der Geruch der Kulturen ist schwach rettigartig.

Nach einem Monat werden Perithezien gebildet, welche bei Einsporenkulturen steril bleiben und einen Durchmesser von 40—50 μ haben. Auch die Perithezien werden in konzentrischen Zonen oder zuweilen sektorweise gebildet. Davidson (1942) hat die Entwicklung der Perithezien näher studiert. Asci hat er auch bei jungen Perithezien nicht gefunden. Sie bestehen nach ihm nur aus einer Plasmamembran, welche gleichzeitig mit dem Reifen der Ascosporen verschleimt wird. In nicht ganz reifen Perithezien wurden die Ascosporen in Gruppen zu 8 in der Perithezienhöhlung gefunden.

Siemaszko's (1939) Beschreibung dieser Art lautet wie folgt:

Peritheciis superficialibus, brunneis, contextu pseudoparenchymatico, parce hirsutis vel levibus, subglobosis, 84—140 μ altis, 74—125 μ diam., rostro 98—140 μ longo, 14—20 μ lato, apice ciliis brevissimis, hyalinis, conoideo collapsis ornato; ascis diffluentibus, ascosporis hyalinis, filiformi-acicularibus, utrinque attenuatis, curvulis, 8—10 (12,5) × 1—1,5 μ, maturitate per rostrum expulsis; sclerotiis absentibus.

Hab. in cortice interna et ligno Piceae excelsae ab Ipide typographo occupatae, Bialowieza, Poloniae.

Ophiostoma minutum ist leicht erkennbar durch die sehr kleinen, braunen Perithezien, mit breitem Halse und konischem Zilienkranze und langen spindelförmigen Ascosporen. In Kultur unterscheidet es sich durch sein sehr langsames Wachstum und sein weisses, glänzendes, oft in konzentrischen Zonen wachsendes Myzel von anderen *Ophiostoma*-Arten.

Durch die Form seiner Ascosporen weicht *O. minutum* entscheidend von allen anderen *Ophiostoma*-Arten ab, die in dieser Hinsicht zeimlich einheitlich sind. Im Aufbau seiner Perithezien und in der Entwicklung der Asci scheint es aber den Arten der Gattung *Ophiostoma* so nahe zu stehen, dass es zunächst als zu dieser Gruppe gehörend betrachtet werden muss.

Als Bläeupilz hat diese Art keine Bedeutung.

2. **Ophiostoma polonicum** Siem.

Fundort: Hofors (Gästrl.), auf berindetem, von Borkenkäfern angegriffenem Fichtenholz.

Ophiostoma polonicum ist von Siemaszko (1939) aus Polen als ein zufälliger Begleiter von *Ips typographus* beschrieben worden.

Unserem Material nach gehört es zu den mehr sekundären Arten, die die alten Insektengänge besiedeln. Er ist zusammen mit *Ips typographus, Acanthocinus aedilis* und *Tetropium* sp. gefunden worden. Unsere Reinkulturen stimmen gut überein mit SIEMASZKO's Beschreibung und Originalkulturen.

O. polonicum bildet auf Malzagar ein dichtes, anfangs blaugrünes, später graubraunes, zottiges, ca. 3—5 mm hohes Luftmyzel. Das Wachstum ist langsamer als sonst bei der *Grosmannia*-Gruppe, 6,0 cm. Geruch fehlt. Das Substratmyzel ist bläulichgrün, bei älteren Kulturen sehr dunkel schwarzgrün. In jungen Kulturen werden *Leptographium*-Konidienträger gebildet, aber sehr spärlich. Die Konidienträger sind klein, unansehnlich, bei unserem Material mit einem höchstens 100 µ langen Stiele (bis 500 µ nach SIEM.), oben einen nach *O. penicillatum*-Typ verzweigten Pinsel tragend, mit ovalen, hyalinen Konidien, 5,3—10 × 2—4 µ, Mittel 8,0 × 2,6 µ (4,4—8 × 2—4—5 µ nach SIEM.). Die Konidien sind in der Form und Grösse ebenso variierend, wie es bei der *Grosmannia*-Gruppe gewöhnlich ist, aber sie sind bei *O. polonicum* durchschnittlich breitoval und von mittlerer Grösse.

Einsporenkulturen bilden schon nach 4—5 Tagen zahlreiche subsphäroidische Perithezien, gleichzeitig mit einer starken sterilen Luftmyzelentwicklung. Die gerade reifgewordenen Perithezien sind mehr hoch als breit, 240 × 227 µ, später werden sie mehr abgeflacht, 250—450 µ (Mittel 340 µ) im Durchmesser, und sind mit langen grauen Haaren besetzt. Der Perithezienhals ist (500) 740—1250 µ lang (340—1200 µ SIEM.), unten 42—51 µ breit (40—50 µ SIEM.), oben 12—28 µ breit (17,5—30 µ SIEM.), mit 11—16 langen, hyalinen, allmählich zugespitzten Zilien, 20—60 × 2 µ (30—70 µ SIEM.). Ascosporen sind bohnenförmig, breit oval, etwas gekrümmt, hyalin, 5,2—7,0 × 2,5—3,6 µ (6,5 × 2,2—2,5 µ SIEM.) mit dicker Schleimhülle. Ascosporen werden in einer gelblichen Schleimmasse, die sich etwas leichter als bei anderen *Ophiostoma*-Arten im Wasser löst, von dem Zilienkranze festgehalten. Asci schnell vergehend.

Die Beschreibung von SIEMASZKO lautet folgendermassen:

Mycelio fuscobrunneo; peritheciis obscure-brunneis, subsphaeroideis, hirsutis, 240—400 µ altis, 250—450 µ diam.; rostro 340—1200 µ longo, inferne 40—50 µ, superne 17,5—30 µ crasso, apice 12—20 filamentis hyalinis, 30—70 µ longis, acutis coronato; peritheciis sub cortice immersis rostro destituis, levibus; ascis effimeris, ovalibus, ascosporis membrana gelatinosa vestitis, late ellipsoideis, singularibus hyalinis, massaque pallide lu-

teolis, 6,5×2,2—2,5 μ. Status conidicus rarissime in culturis formans; hyphis fertilibus hyalinis, conidiis ovalibus hyalinis apicaliter et lateraliter gerentibus; conidiophoris erectis fuscis, 500 μ longis, superne pallidioribus et penicillatim ramosis, conidiis ellipsoideis, hyalinis, 4,4—8×2—4 (5) μ, globulum mucosum formantibus.

Hab. in cortice lignoque Piceae excelsae, Ipide typographo socio in silvis Bialowieza (ipse legi) et in ligno piceino in silvis districtionis Lomza (leg. P. Rutkowski) in Pŏlonia.

Ophiostoma polonicum ist eine interessante Art, weil sie im Gegensatz zu den meisten *Ophiostoma*-Arten in Kultur nur selten Konidien, desto mehr aber Perithezien bildet. Dasselbe scheint der Fall unter natürlichen Bedingungen zu sein. Morphologisch stellt *O. polonicum* eine gute Übergangsform zwischen *Ophiostoma*-Arten s. str. und Arten der *Grosmannia*-Gruppe dar. Durch ihre lang- und schmalhalsigen Perithezien, deren Hälse aus länglichschmalen zylindrischen Zellen bestehen und an der Spitze mit langen hyalinen Zilien besetzt sind, gehört diese Art zu der erstgenannten Gruppe, durch ihre *Leptographium*-Konidienform, Myzelcharaktere und Wachstumsweise zur *Grosmannia*-Gruppe. Ökologisch unterscheidet sie sich wieder von den typischen *Grosmannia*-Arten, indem sie kein Begleiter der primären Borkenkäfer ist, sondern auf schon lange gelagertem Holze auftritt. *O. polonicum* ist ein gutes Beispiel dafür, dass man keine Perithezien charaktere finden kann, mittels welcher man die Gattungen *Ophiostoma* s. str. und *Grosmannia* trennen könnte.

O. polonicum verursacht eine starke Missfärbung, wurde aber nur selten gefunden.

3. **Ophiostoma canum** (Münch.) Nannf.

Fundorte: von Västerbotten bis Südschweden, allgemein auf dünnrindigen Kieferstöcken, die von dem Borkenkäfer *Blastophagus minor* angegriffen sind.

Ophiostoma canum wurde von Münch (1908) beschrieben und ist danach nicht mehr gefunden worden, so dass seine Existenz in Frage gestellt wurde. Mehrmals wollte man diese Art als eine anormale Wuchsform von *O. piceae* betrachten (Zach 1929, Nannfeldt 1934). Wie eigene Untersuchungen es zeigen (Mathiesen 1950), stellt dieser Pilz eine wohldefinierbare Art dar, mit charakteristischer Sporenform und -grösse, die nicht von äusseren Bedingungen

abhängig sind. In Schweden ist dieser Pilz sehr gewöhnlich, und man findet ihn konstant auf Kiefernstämmen, die von *Bl. minor* befallen sind; anderswo als auf solchen Stämmen hat man ihn bisher in keinem einzigen Falle angetroffen.

Die Myzelkonidien von *O. canum* sind hyalin, rund, ziemlich variierend in der Grösse, durchschnittlich 85 µ (7,2—10,4 µ) im Durchmesser und keimen hefeartig oder mit einem Keimschlauche aus. Die Kulturen sind anfangs hyalin, werden vom 5. Tage an hell- bis mittelbraun. Myzelkonidien werden lateral oder terminal an Hyphen von variierender Länge gebildet, meist zu mehreren nebeneinander, kleine *Cephalosporium*-ähnliche Köpfchen bildend. Das Luftmyzel ist ziemlich spärlich und bildet sehr zahlreiche Konidien. Die Wachstumsgeschwindigkeit ist 3,0 cm, Geruch schwach bienenwachsartig.

Vom 5. Tage an werden Graphien gebildet, die 400—800 µ hoch sind (in Insektengängen bis 1200 µ gemessen), und auf einem 20—30 µ dicken, hell- bis dunkelbraunen Stiel einen weissen, kugeligen, bei jungen Kolonien schleimigen Kopf, 80—1500 µ (Mittel 110 µ) im Durchmesser, tragen. Die *Graphium*-Konidien sind hyalin, rund und von sehr variierender Grösse, etwas kleiner als die Myzelkonidien, 7,6 µ (4,2—11,5 µ) im Durchmesser. Sowohl in Myzel- wie in Graphiumkonidien findet man mehrere kleine Öltropfen. Die *Graphium*-Köpfchen trocknen nach za. 30 Tagen aus und bekommen ein kreidiges Aussehen, ebenfalls charakteristisch für diese Art.

Perithezien wurden bisher nur in einzelnen Fällen auf dem Holze gefunden. Sie sind schwarz, fast haarlos, 185 µ hoch und 156 µ breit, mit einem leicht unregelmässig gebogenen Halse, 850 µ lang und 28 µ breit an der Basis und 17 µ an der Spitze, mit zahlreichen gleichbreiten, stumpfen hyalinen Zilien von ungleicher Länge (Mittel 22 µ). Ascosporen nierenförmig, 6,5 × 3,0 µ.

Da von Münch nur eine Kolektivbeschreibung für die *pilifera*-Gruppe gegeben wurde, wird hier eine neue Beschreibung für die Art gegeben.

Ophiostoma canum (Münch.) Nannf.

Mycelium primum hyalinum, brunnescens, demum brunneum, supra e conidiis albo-pulverulentum. Perithecia nigra, fere glabra, subsphaeroidea, 156 µ diam., 185 µ alta, rostellis 850 µ longis, e basi 28 µ in apicem 17 µ diam. attenuatis, circum ostiolum filamentis irregularibus hyalinis ad 22 µ longis praeditis; ascosporis hyalinis reniformibus, paulo curvatis, 6,5 ×

3,0 μ. Graphia graegaria, stipitibus brunneis, 400—800 (1200) μ altis, 20—30 μ crassis, superne dilatato-capitatis, ibique globulo mucoso albo ferentibus; conidiis hyalinis, globosis, 7,6 (4,2—11,5 μ) μ diam. Conidiis secundariis hyalinis, caespitosis, globosis, 8,5 μ (7,2—10,4 μ) diam.

Ophiostoma canum ist an seinen grossen, runden Konidien, welche bei verschiedenen Wachstumsbedingungen unverändert bleiben, leicht erkennbar. Dieser Pilz wird meist in seiner *Graphium*-Form gefunden. Auf dem Holze wächst er schnell, eine intensive Verblauung hervorrufend. Er ist einer der häufigsten und schädlichsten Bläuepilze in Schweden.

4. **Ophiostoma olivaceum** n. sp.

(Abb. 2, a—g.)

Fundorte: Hällnäs (Vb.), Hofors (Gästrl.), auf Kiefern.

Ophiostoma olivaceum, eine Art mit *Graphium*-Nebenfruchtform, kommt in den Larvengängen des Bockkäfers *Acanthocinus aedilis* in den Kiefernstämmen vor. Die Graphien und Perithezien dieses Pilzes wurden in August—September in den Larvengängen und Puppenwiegen gefunden, und das Myzel wird während dieser Zeit einige cm tief um die Larvengänge im Holz herum gefunden, dort eine schwach grünlichblaue Verfärbung verursachend.

Die Reinkultur von *Ophiostoma olivaceum* verläuft wie folgt. Die Konidien wachsen mit einem Keimschlauch aus. Die jungen Myzelien sind anfangs hyalin und werden nach 4—5 Tagen schwach gelblichgrün. Die Farbe der älteren Kulturen wird dunkel olivgrün bis schwärzlich, mit einem 0,6—1 cm breiten hyalinen Rand. Das Luftmyzel ist anfangs spärlich, ebenso spärlich sind die Myzelkonidien, welche an Hyphen von variierender Länge anfangs nach *Cladosporium*-, nachher nach *Cephalosporium*-Typ entstehen. Die Bildung der Myzelkonidien geschieht in gleicher Weise wie bei mehreren *Ophiostoma*-Arten z. B. bei *O. piceae*. Die Wachstumsgeschwindigkeit beträgt 2,8 cm in 10 Tagen.

Die Myzelkonidien sind hyalin, breitoval und ziemlich gross, im Mittel 5,1 × 2,4 μ, mit sehr kleinen Öltropfen. Die Hyphen sind schmal, Lufthyphen 2,8—4,2 μ, Substrathyphen 2,0—7,1 meist 2,8 μ breit, langzellig.

Die charakteristischen Graphien werden vom vierten Tage an gebildet, sind sehr zahlreich, kurz und steif, mit einem rotbraunen bis schwarzbraunen dicken bis sehr dicken, oft knolligen Stiele aus

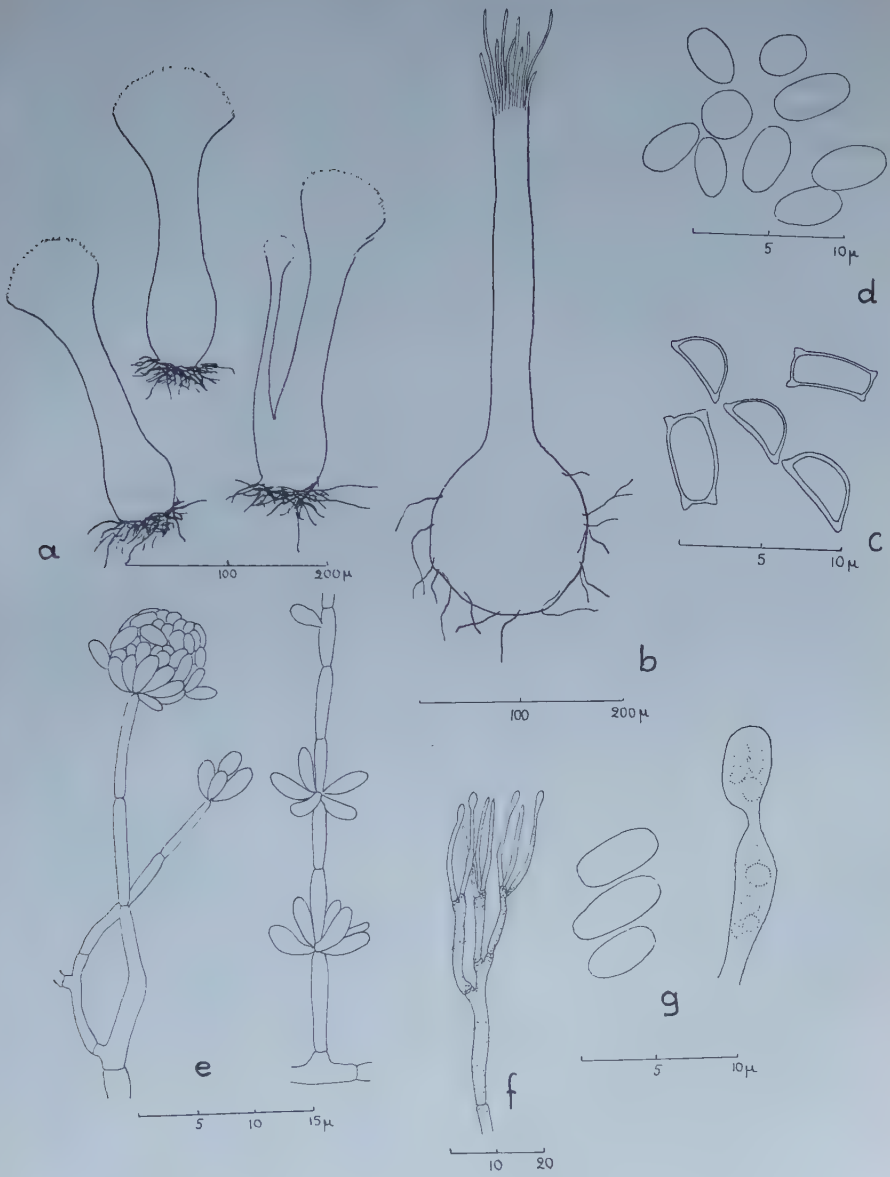

Abb. 2. *Ophiostoma olivaceum* n. sp.: a) Graphien, b) Perithezium, c) Ascosporen, d—e) Myzelkonidien, f—g) Bildung der Graphium-Sporen.

agglutinierten Hyphen. Das obere Drittel des Stieles mit dem garbenförmigen konidientragenden Teil ist hyalin. Der konidientragende Teil ist kurz und sehr reichlich verzweigt. Die terminalen, konidientragenden Verzweigungen sind 6—9 μ lang, < 2 μ breit und stehen zu 2—3 in Wirteln. Die Graphien sind mit einem 74 (43—142) μ breiten, 316 (255—368) μ hohen Stiel versehen und haben ein Köpfchen von 76 (57—43) μ Höhe und 180—1200 μ Durchmesser. Die Graphiensporen sind breitoval, 3,9 × 2,6 (3,21—4,2 × 1,9—3,0) μ, hyalin und mit sehr kleinen Öltropfen. Die Konidien werden auf den Graphien in wässerigen Schleimtröpfchen gesammelt, die bei ganz jungen Graphien wasserklar sind, bei ausgewachsenen Graphien durchsichtig hell grünlichgelb werden und bei alten Graphien milchartig gräulich gelb sind, bis sie zu einer bräunlichen Masse eintrocknen.

Nach der Kulmination der Graphienbildung beginnt nach 12—16 Tagen von den Mitten der Kolonien aus eine sekundäre Luftmyzelbildung. Dieses sekundäre Luftmyzel, welches später die ganze Myzeloberfläche bedeckt, wird aus langen, schmalen sterilen Hyphen gebildet, die sich zu 2—10 Hyphen dicken Myzelsträngen vereinigen und den Kolonien ein graues, zottiges Aussehen geben. In diesem Stadium werden neue Graphien nur langsam gebildet. Nach der sekundären Luftmyzelbildung beginnt die Perithezienbildung bei 2—3 Wochen alten Kulturen. Die sekundäre Luftmyzel- und Perithezienentwicklung kann bei einigen Stämmen auch unterbleiben, und die Graphienbildung dauert länger. Die Kulturen verlieren nach einigen Monaten, also nach 4—5 Umimpfungen, das Vermögen, Perithezien zu bilden. Einsporenkulturen bilden keine Perithezien, sondern nur zahlreiche Graphien.

Die Perithezien sind braunschwarz, mit einem Stich ins Rötlichbraune, sind etwas mehr hoch als breit, 182 μ hoch, 177 μ breit, kahl, mit ziemlich dickem zylindrischem Hals, der 500 (430—540) μ lang, unten 40 μ und an der Spitze 37 μ breit ist. Die Halsspitze trägt sehr unregelmässige, mehrzellige, 40—80 μ lange und 4 μ breite, bräunliche Zilien. Die Ascosporen sind im Profil gekrümmt-elliptisch, an beiden Enden zugespitzt, und haben eine Schleimhülle, die sich an den Sporenenden als kurze Anhängsel fortsetzt. In Dorsalansicht sind sie elliptisch, mit 4 Anhängseln. Sie sind in der Form ähnlich denen von *O. ips* (Rumbold 1936, Fig. 5). Die Grösse der Ascosporen im Profil beträgt 5,7 × 3,3 μ, inkl. Schleimhülle. Die Sporen werden eingebettet in zähem Schleim, als schmale, zu-

sammenhängende, 1—2 Sporen breite Ranken aus dem Perithezienhalse ausgepresst und sammeln sich als gelbliche Klumpen auf dem Zilienkranze.

Ophiostoma olivaceum n. sp.

Mycelium primum hyalinum, dein olivaceo-viride, demum obscurissimum, ad substratum adpressum, hyphis mediocribus 3,0—4,2 μ diam.; mycelium conidioferum fere invisibile. Graphia mox formans. Perithecia obscure-brunnea, fere glabra, subsphaeroidea, 182 μ alta, 177 μ diam., rostellis fere cylindricis, 500 (430—540) μ longis, basi 40 μ, apice 37 μ crasso, circum ostiolum filamentis subbrunneis irregularibus 40—80 μ longis, 4 μ latis praeditis; ascosporiis hyalinis, membrana gelatinosa vestitis, reniformibus, 5,7 × 3,3 μ (cum membrana), e hyalino in massa pallide luscentibus. Graphia graegaria, stipitibus rigidis, brunneis, 316 (255—368) μ altis, 74 (43—142) μ crassis, interdum e hypha singula oriundis, superne dilatato-capitatis ibique globulum mucosum luteo-viridem 180—1200 μ diam. ferentibus; conidiis hyalinis, late ovalibus, solitarie acrogenis, 3,9 × 2,6 (3,2—4,2 × 1,9—3,0) μ. Conidia secundaria caespitosa, hyalina, ovalia, 5,1 × 2,4 μ, basi attenuatis, e conidiophoris longitudine variabili apice denticulis sporigeris congestis.

Dieser Pilz unterscheidet sich durch seine kurz- und dickstieligen Graphien mit grünlichgelben Köpfchen, olivgrünes Myzel und kleine, ziemlich kurzhalsige Perithezien mit langen irregulären Zilien von allen anderen Arten der *Graphium*-Gruppe. Am nächsten steht er *O. obscurum* (*Ceratostomella obscura* Davids.), mit dem er sich aber nach Vergleichung der Kulturen nicht als identisch erwies. Auch der Beschreibung nach weicht *O. obscurum* von dem beschriebenen Pilze ab, indem er als Nebenfruchtform nach Davidson *Graphium*-ähnliche Koremien, etwa von dem Typ von *O. ips*, bildet, unser Pilz aber regelmässige Graphien hat. Die Perithezien stimmen ziemlich überein, nur sind die Zilien bei *O. olivaceum* von einem anderen Typ als bei *O. obscurum*.

Als Bläuepils hat *O. olivaceum* keine grössere Bedeutung.

5. Ophiostoma floccosum n. sp.

(Abb. 3 a—e; Abb. 4.)

Fundorte: Hällnäs (Vb.), Hofors (Gästrl.), Enebyberg (Uppl.), sporadisch auf Fichten- und Kiefernholz, sowohl zusammen mit anderen Luftbläuen auf mechanisch beschädigten Stämmen als auch zufällig in alten Frassbildern von *I. typographus*, *Pityogenes chalcographus* und *Acanthocinus aedilis*.

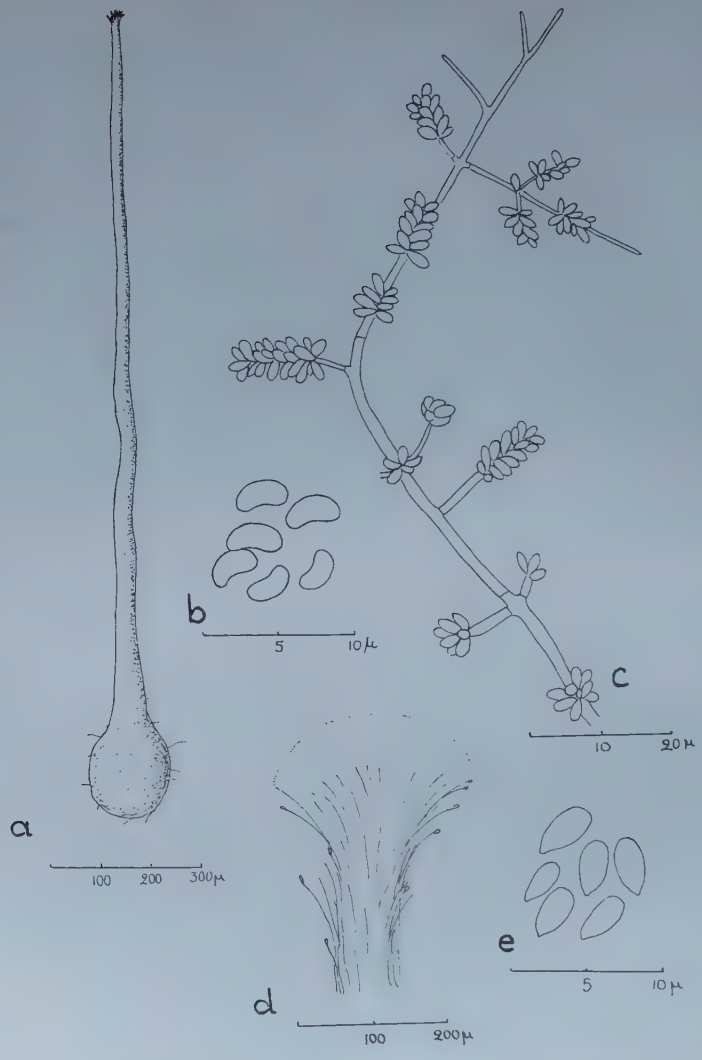

Abb. 3. *Ophiostoma floccosum* n. sp.: a) Perithezium, b) Ascosporen, c) Lufthyph mit Konidien, d—e) Graphium und Graphium-Sporen.

Ophiostoma floccosum wird meist in der *Graphium*-Form gefunden. Im September wurden einigemal auf dem Holze neben den eingetrockneten Graphien auch zahlreiche Perithezien gefunden, von denen die Einsporenkulturen der Ascosporen wieder typische Graphien und einigemal auch Perithezien produzierten. Die Graphien stimmen mikroskopisch mit dem von GOIDÀNICH (1936) be-

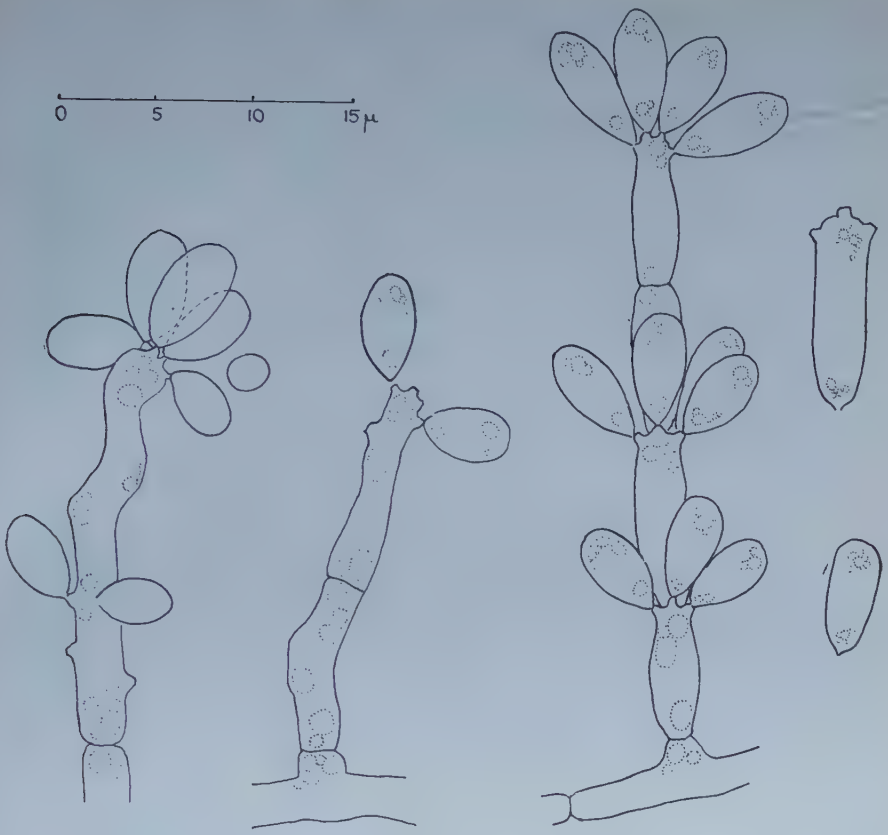

Abb. 4. *Ophiostoma floccosum* n. sp.: Bildung der Myzelkonidien.

schriebenen *Graphium silanum* überein, aber durch die hellbraune Farbe des Myzels und durch das langsame Wachstum unterscheidet sich dieser Pilz von Originalkulturen von *O. silanum,* die fast schwarzbraunes Myzel und schnelles Wachstum zeigen. Das Perithezienstadium von *Graphium silanum* ist bisher unbekannt.

Die Reinkultur von *Ophiostoma floccosum* verläuft folgendermassen. Das Myzel wird von schmalen, bis 3 µ breiten Hyphen gebildet, ist langsamwachsend, 2,0 cm in 10 Tagen. Das Substratmyzel ist anfangs hyalin und wird nach einigen Tagen hell sepiabraun, mit einem 0,4—0,5 cm breiten hyalinen Rande. Die Farbe wird intensiver bei älteren Kulturen, wo das Substratmyzel schwarzbraun werden kann. Die Farbe erinnert an die von *O. piceae,* ist aber dunkler. Der Geruch ist schwach honigartig. Das Luftmyzel ist an-

fangs weiss, wird danach hellgrau-gelblichgrau und ist viel reichlicher als bei *O. piceae,* wollig an den zentralen Partien.

Die Myzelkonidien sind sehr zahlreich und entstehen entweder einzeln, pleurogen an weiterwachsenden Hyphen, oder werden akrogen an sehr kurzen Hyphen, die nicht weiterwachsen, nach *Cephalosporium*-Typ gebildet, oder sie entstehen sehr oft wirtelig um weiterwachsende Hyphen. Das Vorherrschen der Konidien von letzterem Typus gibt dem Myzel schon bei kleineren Vergrösserungen ein charakteristisches Aussehen. Die Myzelkonidien, sowohl akrogene wie pleurogene werden an deutlichen, breiten und stumpfen kegeligen Höckerchen gebildet, ähnlich denen des Genus *Rhinotrichum (Hyphales Mucedinacae).* Solche auffallende breite Höckerchen sind nach Goidànich (1936, p. 244) ein charakteristisches Merkmal für *Graphium silanum.*

Die Myzelkonidien sind eiförmig, grösser und dabei breiter als bei *O. piceae,* im Mittel 6,8 × 3,9 µ. Die oft zu drei an kurzen Höckerchen an Hyphenenden gebildeten Konidien können in einigen Fällen weiter wachsen, bis 9,4 × 4,2 µ, und wieder terminal an ähnlichen stumpfkegeligen Höckerchen können 2—3 Konidien absprossen usw., wodurch der Konidienapparat ein dendritisches Aussehen erhält. Eine gute Abbildung von ähnlichen Konidienformen bei *Graphium silanum* findet man bei Goidànich (1936, S. 245). Dieser mehrfach verzweigte Konidienapparat fällt im Wasser sogleich auseinander.

Die *Graphium*-Synnemata wachsen aus einem dicht geflochtenen Hyphengemenge hervor und haben einen dunklen, rötlichbraunen bis schwarzbraunen Stiel, der 400—500 µ hoch und 50—60 µ breit ist. Der obere konidientragende Teil der Graphien ist hyalin, diskusartig ausgebreitet und 180—350 µ breit. Die Graphien sind lockerer aufgebaut als bei *O. piceae;* die terminalen Verzweigungen sind weniger regelmässig und von sehr verschiedenen Länge, und kurze, konidientragende Hyphen findet man auch an dem Stiele unter dem eigentlichen Diskus. Die terminalen, konidientragenden Äste stehen meist zu drei in Wirteln, sind ungefähr gleichlang, gegen das Ende zugespitzt, und bilden akrogen 1—3 Konidien. Die *Graphium*-Konidien sind kleiner und schmaler als die Myzelkonidien, hyalin, mit undifferenziiertem Inhalt, 4,0 × 2,2 µ. Sie keimen in 12 Stunden mit einem polaren Keimschlauch aus oder sprossen hefeartig. Die Konidien werden auf den Graphien in Schleimtropfen gesammelt, welche anfangs gelblich wasserklar sind,

danach durchscheinend hellgelb bis honiggelb werden und bis zum Eintrocknen durchsichtig bleiben und nicht milchig werden wie bei *O. piceae*. Die eingetrockneten Konidienmassen sind bernsteingelb. Oft findet man alle Übergänge von den typisch ausgebildeten Graphien bis zu den einfachen Konidienträgern mit Stielen, die nur aus einer Zellreihe bestehen, die aber nicht zu den *Scopularia*-Typen gehören.

Die Perithezien sind schwarz, kahl, rund, 155 (110—182) µ im Durchmesser, mit einem 940—1600 µ langen, unregelmässig gebogenen Halse, der an der Basis 36—70 µ, an der Spitze 12—20 µ breit ist. Zilien sind meist 16 an der Zahl, 10—12,5 µ lang und 2,8 µ breit. Ascosporen werden in schleimigen Ranken ausgepresst und sind einzeln hyalin, in Masse anfangs weiss, dann gelblich. Die Sporen sind nierenförmig, 3,5 × 1,7 µ (3,3—4,7 × 1,5—2,6 µ). Asci schnell verschleimend.

Ophiostoma floccosum n. sp.

Mycelium primum hyalinum, dein brunneum, demum obscurissimum, mycelium aerophilum griseum vel luteo-griseum, caespitosum; conidiis numerosis acrogenis vel pleurogenis, apice denticulis sporogenis late conicis conidiis late-ovatis, 6,8 × 3,6 µ, aliquando in fructificationibus arboriformibus dispositis. Perithecia atra, glabra, sphaeroidea, 155 (110—182) µ diam., rostellis atris, 940—1600 µ longis, basi 36—70 µ, apice 12—20 µ crassis, ciliis hyalinis, 10—12,5 × 2,8 µ; ascosporiis reniformibus hyalinis, 3,5 × 1,7 (3,3—4,7 × 1,5—2,6) µ, e hyalino in massa pallide brunneis. Graphia graegaria, stipitibus longis, brunneis, 400—500 µ altis, 50—80 µ crassis, interdum e hypha singula oriundis; hyphiis synnematibus saepe non agglutinis; conidiis ramis penicillatis enatis, hyalinis, 4,0 × 2,2 µ, globulum mucosum luteum ferentibus.

In seinem *Graphium*-Stadium ist dieser Pilz ähnlich *O. piceae*, ist aber durch die wasserklaren, gelben *Graphium*-Köpfchen und das reichliche, wollige Luftmyzel schon makroskopisch erkennbar. Mikroskopisch unterscheidet er sich durch die kleineren und kahlen Perithezien, mit recht langen Hälsen und breiten stumpfen Höckerchen, an denen die Myzelkonidien gebildet werden.

Als Bläuepilz hat dieser Pilz keine grössere Bedeutung, weil er sporadisch und meist gemischt mit anderen Arten vorkommt.

6. **Ophiostoma clavatum** n. sp.

(Abb. 5 a—f.)

Fundorte: von Norrbotten bis Dalarna, oft auf Wipfelstöcken von Kiefern, die von *Ips acuminatus* befallen sind.

Ophiostoma clavatum gehört zu den konstanten Begleitern des Borkenkäfer *Ips acuminatus* und ist in den nördlichen Teilen des Landes sehr gewöhnlich. Dieser Pilz hat ein sehr stark pigmentiertes Myzel. In Reinkultur auf Malzagar ist die Farbe des Myzels schwarz, manchmal ins Grünliche, manchmal ins Bräunliche spielend. In den Larvengängen und Puppenwiegen bildet *O. clavatum* im Juli—August zahlreiche Graphiumähnliche Koremien mit einem keulenförmigen Köpfchen. Später, Ende Juli—August, erscheinen auch Perithezien in den Gängen und auf dem Holze unter der Rinde. Dabei erscheinen die Perithezien oft um die Insektengänge tief innen im Holze, so dass nur die Halsspitzen frei in die Gänge hineinragen. Die ziemlich kleinen, wenn auf freiem Holze entstehend, ziemlich kurz- und schmalhalsigen Perithezien mit langen, braunen, gekrümmten Zilien sind sehr charakteristisch für diese Art und ebenso die eigentümlichen *Graphium*-Koremien.

Die Sporen keimen oft hefeartig, mit einer polaren Knospenzelle, aus oder teilen sich in der Mitte in zwei gleichgrosse Tochterzellen. Teilweise keimen die Konidien mit einem Keimschlauch aus. Das Myzel wird von sehr schmalen, im Mittel 2,5 µ breiten, stark und unregelmässig verzweigten Hyphen gebildet. Das Myzel ist anfangs hyalin und wird danach grünlich bis bräunlichschwarz. In Agarkulturen wird meist nur Substratmyzel gebildet. Das Luftmyzel ist sehr spärlich, gräulich und wird ebenfalls von sehr schmalen Hyphen gebildet. Die Wachstumsgeschwindigkeit ist 7,5 cm in 10 Tagen. Geruch schwach aromatisch oder fehlend.

Die Myzelkonidien sind in Kultur sehr spärlich. Sie werden akrogen an mehrfach wirtelig verzweigten hyalinen Konidienträgern gebildet, sind schleimig und können kleine *Cephalosporium*-Köpfchen bilden. Solche Konidienträger gleichen einzelstehenden konidientragenden Ästen der *Graphium*-Koremien derselben Art. Konidien an Substratmyzel sind zahlreicher und werden in der gleichen Weise gebildet wie an den Lufthypen. Sie sprossen in dem Substrat meist hefeartig und bilden dichte Anhäufungen. Die Form und Grösse der Konidien ist variabel: sie sind unregelmässig eiförmig bis elliptisch oder sogar rundlich; die Grösse beträgt 6,3 × 2,9 (5,1—7,4 × 2,2—4,2) µ. Einsporenkulturen aus Konidien ergeben oft farblose Mutanten.

Auf dem Holze werden zahlreiche Graphiumähnliche Koremien gebildet. In der Kultur sind diese spärlich und werden nur nach den ersten Abimpfungen gebildet. Sie sind 150—500 µ hoch und be-

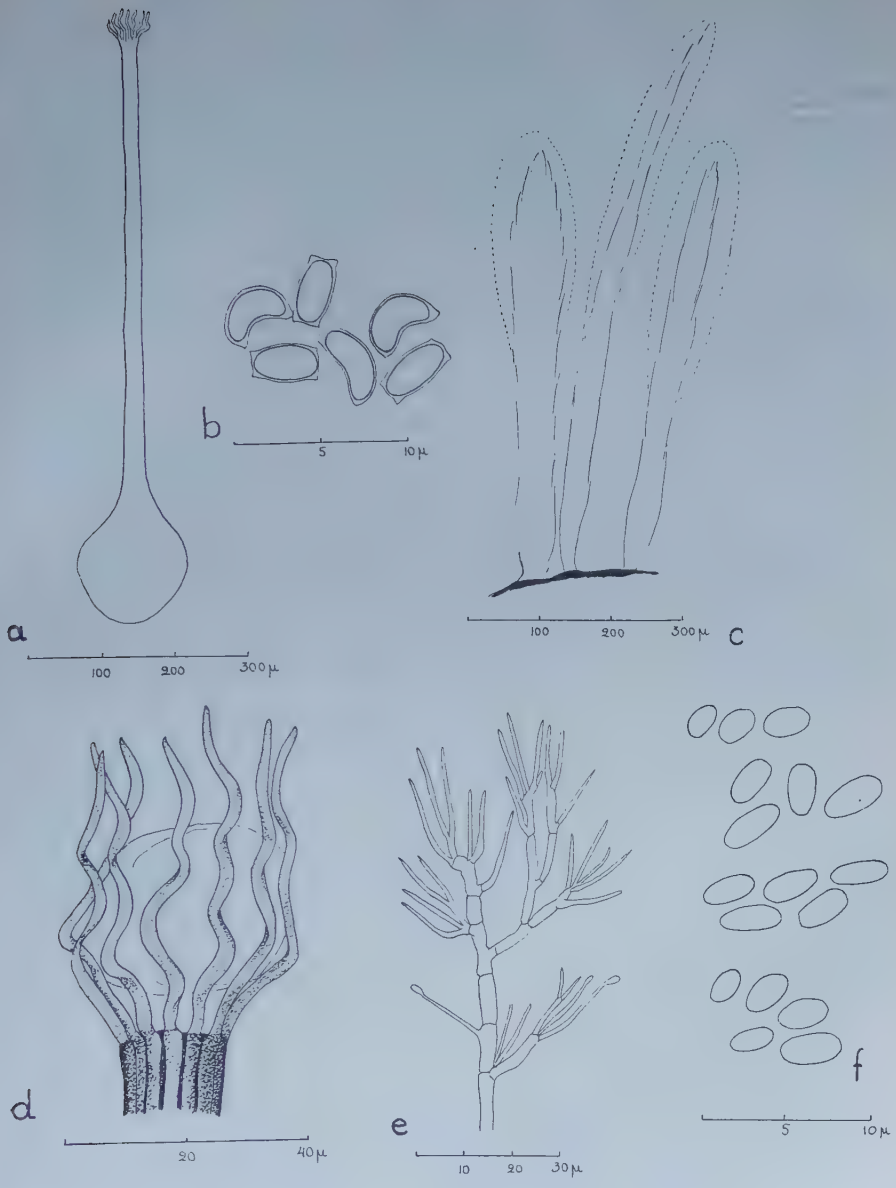

Abb. 5. *Ophiostoma clavatum* n. sp.: a) Perithezium, b) Ascosporen, c) Graphien, d) Zilien am Perithezienhalse, e—f) Myzelkonidien und Konidienträger.

stehen aus einem gleichbreiten dunklen Fusse und einem keulenförmigen hyalinen sporentragenden Teil. Der Fussteil ist aus ziemlich lockeren, dunklen Hyphen aufgebaut und kann manchmal fehlen. In dem oberen hyalinen Teil werden Konidien akrogen an Hyphenzweigen, die unregelmässig auf der ganzen oberen Hälfte der Koremien abgegeben werden, gebildet. Die Konidien sind schleimig und bleiben als keulige schleimige Köpfchen an den Trägern sitzen, bilden aber keine regelmässigen runden Köpfchen wie bei den *Graphium*-Arten. Die Sporen an den Koremien sind ziemlich regelmässig, elliptisch, 3,2 × 1,9 (2,7—3,5 × 1,7—2,1) µ, mit einem kleinkörnigen Inhalt.

Die Perithezien, welche zahlreich auf feuchtem Holze entstehen, in der Kultur aber bisher nur vereinzelt gebildet wurden, sind ziemlich klein, rund, etwas eingedrückt an der Basis, haarlos, braunschwarz, 166 (127—212) µ hoch under 177 (127—238) µ breit. Der Hals ist ziemlich lang und schmal, nach der Spitze hin sich etwas verschmälernd, 566 (453—830) µ lang, an der Basis 35,9 (28,3—45,3) µ und an der Spitze 15,8 (11,3—19,8) µ breit. Der Hals ist stets mit langen, braunen charakteristisch spiralig gekrümmten Zilien versehen, 9—16 (oft 12) an der Zahl, 52,2 (14,0—81,2) µ lang und 2,8 µ breit.

Ascosporen werden in der gleichen Weise gebildet wie bei den anderen *Ophiostoma*-Arten. Die Asci sind schnell verschleimend. Ascosporen sind in der Dorsalansicht langelliptisch, 3,3 × 1,4 µ; in der Seitenansicht zeigen sie die Form von Orangensektionen. Die Sporen bilden einen zähen, weissen Schleimtropfen am Perithezienhalse. Aus den Ascosporen wachsen Myzelien heraus, die typische Myzelkonidien und Graphien produzieren; zu einer Perithezienbildung kam es nur in einzelnen Fällen, und auch dann wurden sie nur vereinzelt gebildet.

Ophiostoma clavatum n. sp.

Mycelium primum hyalinum, demum obscure atro-viride vel atro-brunneum, hyphis septatis irregulariter ramosis, 2,5 µ diam.; mycelium aerophilum ad substratum adpressum, saepe non evolutum; mycelium conidioferum fere invisibile; conidiis secundariis hyalinis, hyphis hyalinis ramosis apicaliter vel lateraliter congestis, 6,3 × 2,9 (5,1—7,4 × 2,2—4,2) µ, saepe mucore coactis. Perithecia (in ligno tarde evoluta, in culturis saepe non visa) obscure-brunnea, subsphaeroidea, glabra, 166 (127—212) µ alta, 177 (127—237) µ diam., rostellis atris, 566 (453—830) µ longis, e basi 35,9 (28,3—45,3) µ in apicem 15,8 (11,3—19,8) µ diam. attenuatis, circum ostio-

lum filamentibus 8—16 longissimis recurvatis, brunneis, 52,2 (14,8—81,2) µ longis, 2,8 µ latis praeditis; ascosporis reniformibus, vel dorsaliter ellipsoideis, 3,3 × 1,4 µ, membrana gelatinosa vestitis. Coremia graphioidea clavata, saepe ramosa, 150—500 µ alta, stipitibus brevibus rigidis, brunneis, 40—200 µ crassis, superne capitulo mucoso hyalino claviformi; hyphiis synnematibus inferne obscuris ramosis, superne pallidioribus et repetite verticillato-ramolusis; ramulis extremis conidium singulum vel plurima gerentibus; conidiis ellipsoideis, 3,2 × 1,9 (2,7—3,7 × 1,7—2,1) µ, mucore congestis.

Ophiostoma clavatum ist sehr typisch in den von *Ips acuminatus* angegriffenen Kiefernstämmen. Dieser Pilz wurde in der früheren Arbeit von Rennerfelt (1950) als eine unbeschriebene Art, unter der Benennung *Ophiostoma I* behandelt. Durch die keulenförmigen Graphien und kleinen, ziemlich kurz- und schmalhalsigen Perithezien mit langen, braunen, gewundenen Zilien, ist diese Art gut unterscheidbar.

O. clavatum verursacht eine starke Verfärbung des Holzes und ist wegen seines häufigen Vorkommens einer der wichtigsten Bläuepilze.

7. **Ophiostoma tetropii** n. sp.

(Abb. 6 a—f; Abb. 7.)

Fundort: Hofors (Gästrl.), in stehenden toten und halbtoten Fichtenstämmen.

Ophiostoma tetropii wurde in den Larvengängen des Bockkäfers *Tetropium* sp. an der Stammbasis überjähriger stehender Fichten, welche durch Borkenkäferangriff getötet waren, gefunden. Der Pilz wuchs nur in der nächsten Umgebung der Larvengänge und Puppenwiegen, und das schwach pigmentierte Myzel verursachte nur eine geringe Bläue. In Kultur gehört *O. tetropii* zu den schnellwüchsigen Typen.

Das Substratmyzel von *Ophiostoma tetropii* ist anfangs hyalin, wird nach 10 Tagen hell gelblichbraun und bleibt so. Später werden Perithezien auf dichteren dunkel-sepiabraunen Myzelanhäufungen gebildet, so dass Stellen mit dichtstehenden Perithezien dunkelbraun erscheinen. Das Luftmyzel ist hell gelblichgrau, kurz und dicht und wie feinkörnig von zahlreichen Myzelkonidien. Nach der Kulmination der Perithezienbildung kann die Kolonie überwachsen werden von einem dichteren und höheren, ebenfalls hellgrauen sekundären Myzel, das ebenso reichlich Konidien produziert. Die Substrathyphen sind bis 10,6 µ breit, die Lufthyphen schmaler, 1,9—3,8 µ breit, oft

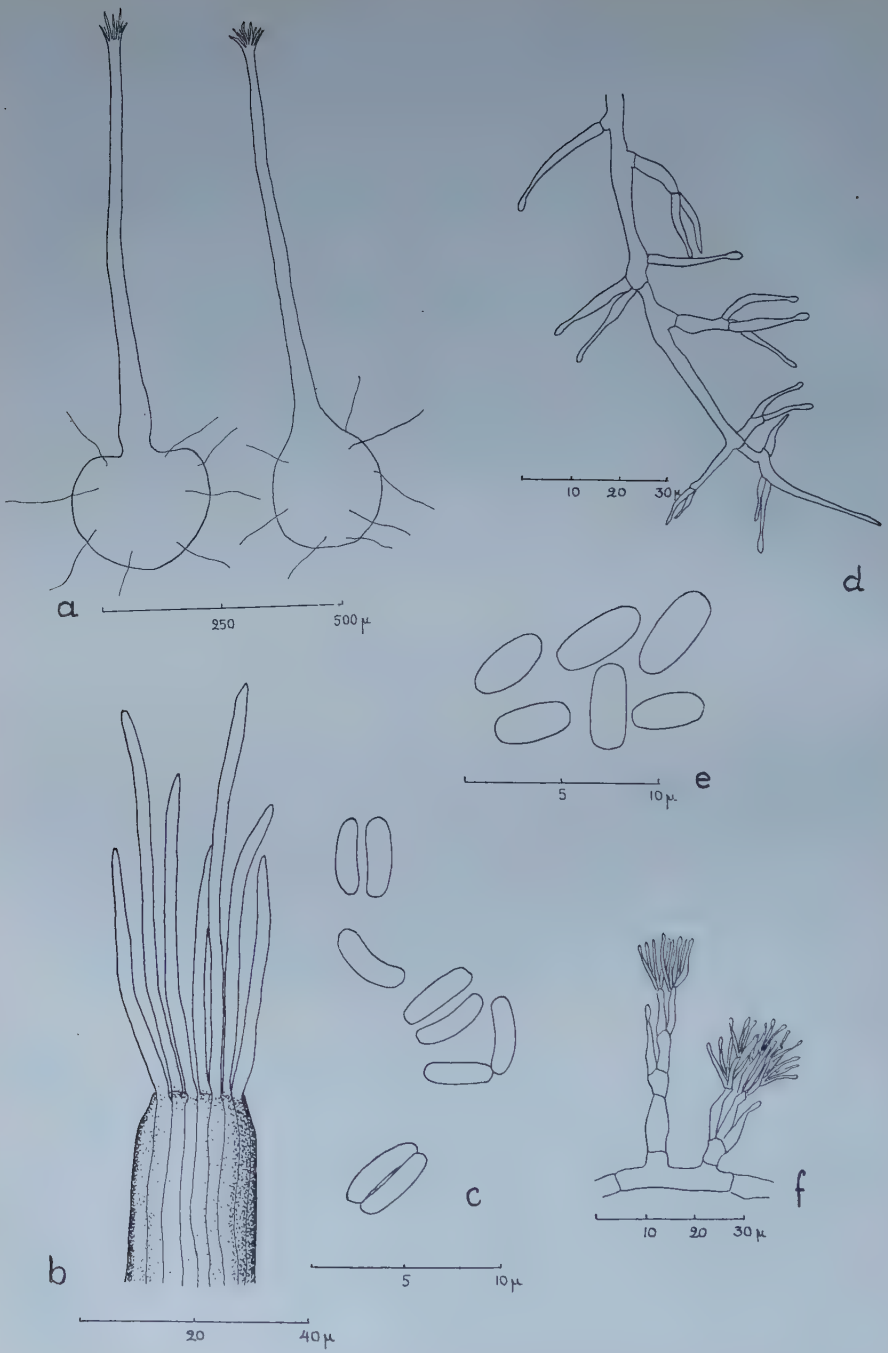

Abb. 6. *Ophiostoma tetropii* n. sp.: a) Perithezien, b) Zilien am Peritheziumhalse, c) Ascosporen, d) Lufthyph mit Konidien, e—f) Konidienträger mit Konidien.

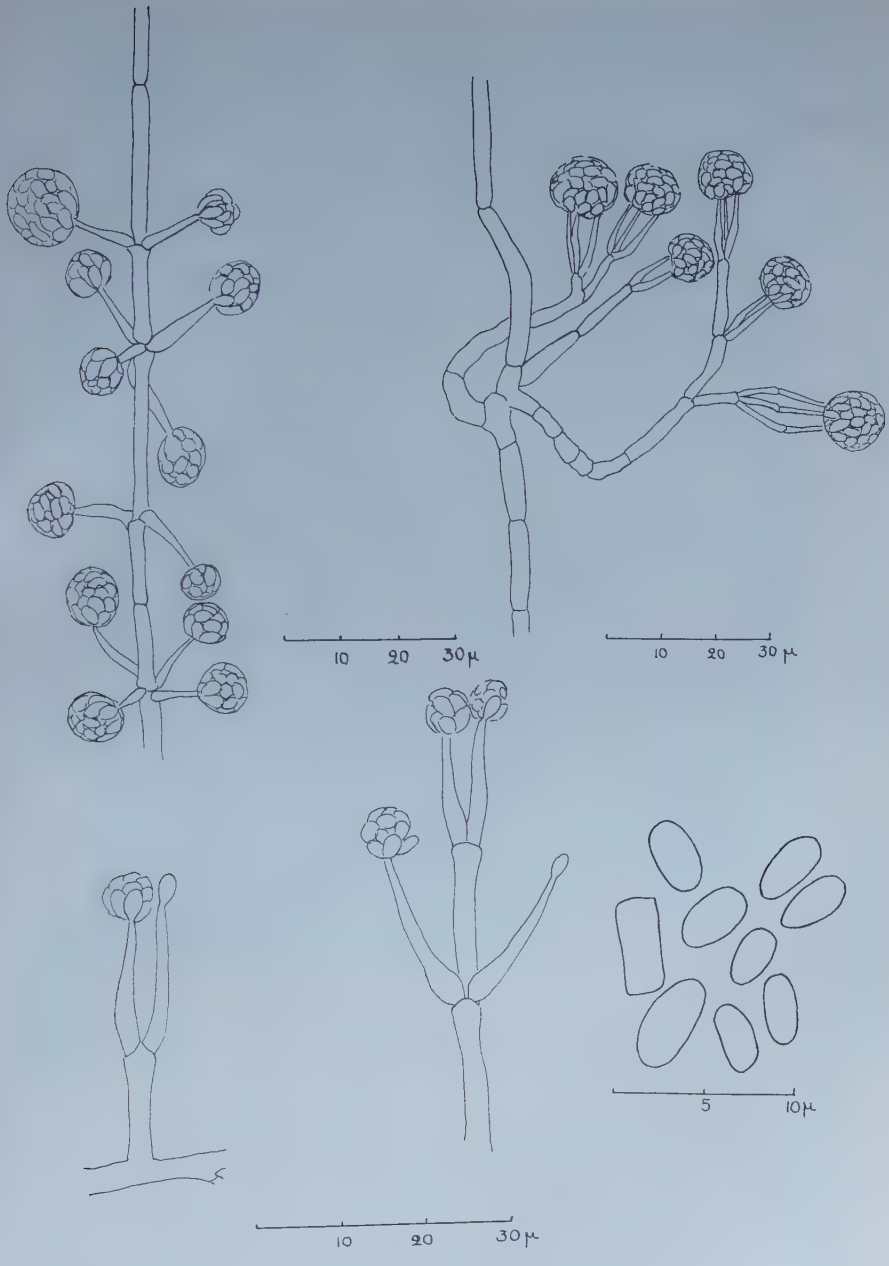

Abb. 7. *Ophiostoma tetropii* n. sp.: Verschiedene Formen der einfachen Konidienträger und Konidien.

vakuolisiert und kollabieren leicht. Die Lufthyphen vereinigen sich oft zu feinen und zarten, locker zusammengewebten Strängen. Wachstumsgeschwindigkeit 8,8 cm in 10 Tagen. Geruch nicht ausgeprägt.

Als Nebenfruchtform findet man hauptsächlich Myzelkonidien von *Cephalosporium*-Typ. Die Art, Myzelkonidien zu bilden, ist recht typisch für *O. tetropii*. Die Konidien werden nämlich an kurzen, einzelligen, hyalinen Tragzellen gebildet, welche meist zu 3—4, aber auch in grösserer Anzahl in Wirteln stehen. Die Konidien werden an den Tragzellen apikal nebeneinander abgeschnürt und sammeln sich zu recht grossen Köpfchen an Hyphenenden. Die Tragzellen können sich zu mehr komplexen Verbindungen vereinigen, indem sie kurze einzellige Äste widerholt abgeben können. Damit werden alle Übergänge von den einfachen Konidienträgern zu den *Scopularia*-artigen Konidienträgern, die nachher beschrieben werden, gebildet. Ausserdem sitzen die Konidien oft wirtelig ohne besondere Tragzellen an den weiterwachsenden Langhyphen, zuweilen dichte ährenförmige Gebilde darstellend. Die Myzelkonidien sind einzellig, hyalin und von sehr ungleicher Grösse und Form. Die mittlere Grösse beträgt 4,7 × 2,3 (4,1—5,2 × 1,8—2,5) µ, die Form ist eiförmig bis zylindrisch oder fast viereckig, manchmal basal zugespitzt und terminal abgeflacht, manchmal an beiden Enden abgerundet.

Ausser Myzelkonidien bildet *O. tetropii* kleine *Scopularia*-ähnliche Konidienträger. Diese sind bis 100, meist 70 µ hoch, 5—8 µ breit und bestehen aus einem 1—2, selten 3—4-zelligen hyalinen, selten braunen, Träger, der oben einen hyalinen *Scopularia*-artig verzweigten Pinsel trägt. Die terminalen, langsam zugespitzten Äste geben acrogen 1 bis mehrere Konidien ab, die durch die schleimigen Membranen zusammengehalten werden, aber nie schon makroskopisch erkennbare grosse Schleimtropfen bilden, wie die *Scopularia*-Arten. Die Konidien an solchen Trägern sind regelmässiger an Form und Grösse, meist langelliptisch, 4,4 × 1,6 (3,8—5,2 × 1,4—1,9) µ.

Auch die Perithezien von *O. tetropii* sind charakteristisch. Diese sind ziemlich gross, schwarzbraun, 311 (226—355) µ breit und 302 (212—383) µ hoch. In Malzagarkulturen sind die Perithezien mit dichten, langen, hellbraunen Haaren besetzt; auf dem Holze sind die Haare weniger auffallend. Der Hals geht bei den jungen Perithezien allmählich in den runden Teil über; bei alten Perithezien, die teilweise die Sporen entlassen haben, werden die Hälse

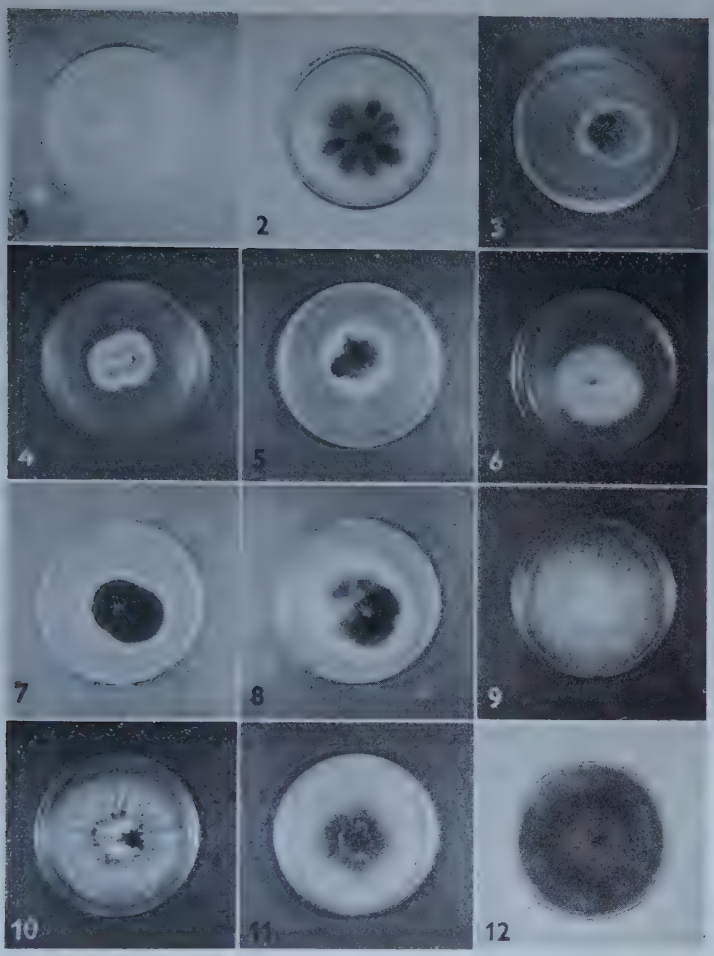

Abb. 8. Wachstum einiger *Ophiostoma*-Arten auf 2,5 % Malzagar nach 10 Tagen. Von links oben: 1) *Ophiostoma minutum*, 2) *O. polonicum*, 3) *O. canum*, 4) *O. floccosum*, 5) *O. olivaceum*, 6) *O. piceae*, 7) *O. clavatum*, 8) *O. clavatum*, 9) *O. tetropii*, 10) *O. coeruleum*, 11) *O. pini*, 12) *O. penicillatum*.

an der Basis eingeschnürt, und der obere Teil des Peritheziums wird um den Hals eingebuchtet, so dass die alten Perithezien mehr abgeflacht erscheinen als die jungen. Der Hals ist lang, im Mittel 906 (594—1179) μ, gegen die Spitze stark verschmälert, an der Basis 50,9 (42,5—58,1) μ breit, oft etwas knollig angeschwollen, an der Spitze 25,2 (17,0—28,3) μ breit. Die Zilien sind nicht sehr zahlreich, meist 12 (6—16) an der Zahl, hyalin, sehr lang und dabei von sehr ungleicher Grösse, steif und nadelförmig, 40—70 × 1—1,5 μ.

Die Ascosporen entstehen in leicht verschleimenden rundlichen Asci; sie sind fast zylindrisch, etwas gebogen, bis bohnenförmig, mit stumpfen Enden, 3,8—4,0 × 1,0—1,4 μ. Die Ascosporen sammeln sich wie bei anderen *Ophiostoma*-Arten zu schleimigen Tröpfchen auf dem Zilienkranze. Solche Sporentropfen sind zuerst gelblichweiss, später gelblichbraun. Der Schleim, in dem die Sporen eingebettet liegen, ist nicht so zähe wie bei den meisten *Ophiostoma*-Arten, und die Sporen werden leichter in Wasser dispergiert.

Ophiostoma tetropii ist homothallisch, und die Perithezienbildung beginnt auf Malzagarkulturen sehr schnell. Bei 10 Tage alten Kulturen findet man schon Perithezien mit voll entwickelten Hälsen, aber mit unreifen Asci. Die Perithezien werden zahlreich gebildet, und selbst bei einige Jahre alten Kulturen ist die Perithezienbildung noch immer lebhaft.

Ophiostoma tetropii n. sp.

Mycelium primum hyalinum, demum pallidum vel brunneum, aerophilum albo-pulverulentum; hyphis fasciculatis; conidiis numerosis irregulariter ovatis, 4,7 × 2,3 (4,1–5,2 × 1,8–2,5) μ, acrogeniis vel pleurogeniis, capitulis minutis hyalinis formantibus. Perithecia brunnea, globosa, pilifera, 311 (212—383) μ alta, 302 (226—354) μ lata, rostellis brunneis, rigidis, 906 (594—1179) μ longis, e basi 50,0 (42,5—58,1) μ in apicem 25,2 (17,0—28,3) μ diam. attenuatis; filamentis ostiolaribus hyalinis setiformibus 40—70 μ longis, acutis. Ascosporia hyalina, cylindrata, leniter curvula, 3,8–4,0 × 1,0—1,4 μ, in globulo apicali mucoso collectis. Asci rotundati diffluentes. Conidiophora minuta penicillata, 70—100 μ alta, e hypha singula oriunda, stipitibus brevibus hyalinis, aliquando pallide brunneis, saepe non evolutis, superne repetite verticillato-ramosis; ramulis extremis hyalinis, conidium unum—plurima gerentibus. Conidia longe ellipsoidea, 4,4 × 1,6 (3,8 – 5,2 × 1,4—1,9) μ; glomerulis sporarum hyalinarum ut in O. pini.

Diese schnellwüchsige *Ophiostoma*-Art ist durch ihr flockig-wolliges Wachstum, kleine hyaline *Scopularia*-artige Konidienträger und grosse, langhaarige Perithezien charakterisiert.

Als Bläuepilz hat er keine grössere Bedeutung, da es in dem Holze nur in der unmittelbarer Nähe der Larvengänge wächst und nicht stark pigmentiert ist.

Summary.

In the present and two previous papers (RENNERFELT 1950, MATHIESEN 1950), the blueing fungi associated with the commonest bark beetles in Sweden have been discussed. It has been established (RENNERFELT, l. c.), that some bark beetles, e. g. *Blastophagus minor, Ips acuminatus, I. typographus* a. o., are constantly followed by blueing fungi. At the time of infestation the adult beetles are carrying spores epi- and endozoically. Other bark beetles, such as *Blastophagus piniperda, Pityogenes chalcographus, P. quadridens* a. o. are only sporadically carrying blueing fungi. In fresh tunnels of the lastmentioned beetles no blueing fungi are found and in old tunnels some common non-specific air-spread fungi, such as *Ophiostoma pini, O. piceae, Pullularia pullulans* a. o. appear. The blueing fungi associated with the first mentioned bark beetles are strongly specific. A good example of such highly spezialized fungi are those associated with the bark beetles *Ips acuminatus* and *Blastophagus minor*. These bark beetles are living under rather similar conditions on top-logs of Scots pine but each of them is always accompanied by its specific fungus, viz. *Bl. minor* by *Ophiostoma canum* and *I. acuminatus* by *Ophiostoma clavatum*. These fungi never accompany other bark beetles.

Even some less common bark-beetles and wood-boring beetles were found to be accompanied by blueing fungi, which were hitherto found only in their galleries (MATHIESEN 1950). So *Acanthocinus aedilis* on Scots pine is accompanied by *Ophiostoma olivaceum* n. sp. and in the tunnels of *Tetropium* sp. on Norway spruce *Ophiostoma tetropii* n. sp. is found. Since these beetles occur more seldom and since their fungous contaminants are growing slowly and are causing only a slight discoloration, these fungi have often been overlooked.

Besides the named *Ophiostoma* species, which are more or less strongly associated with their insect vectors, numerous other *Ophiostoma* species occur in old tunnels and in wooden tissues of infested trees. Among such species *Ophiostoma pini, O. minutum, O. polonicum, O. floccosum, O. piceae, O. multiannulatum,* and *O. coeruleum,* may be named.

The commonest and most damaging fungi associated with bark-beetles on Scots pine are *Ophiostoma canum, O. clavatum* and *Trichosporium tingens;* on Norway spruce *O. penicillatum* is the

commonest fungus. The commonest air-spread blueing fungi on pine and spruce are *Ophiostoma pini, O. coeruleum, O. piceae, Pullularia pullulans,* and *Cladosporium herbarum.*

In the present paper three *Ophiostoma* species hitherto not found in Sweden and four new species are being described. Of the former, *O. minutum* SIEM. is found in Sweden on spruce and pine in old tunnels of various bark beetles. This slowly growing fungus has no significance as a blueing fungus. *O. polonicum* SIEM., with *Leptographium* imperfect stage, occurs on half-dry spruces and is not associated with any particular bark beetle. It causes a deep green stain, but is not very common in Sweden. *O. canum* (MÜNCH) NANNF. is very common in Sweden. It has been constantly isolated from the deeply stained sapwood of pine, following the attack of *Blastophagus minor.* This fungus, whose existence has many times been questioned is through constant morphological and physiological qualities a well characterized species.

Ophiostoma olivaceum n.sp., with a *Graphium* conidial stage, has been found in tunnels of *Acanthocinus aedilis* on pine. This fungus produces a blue-green stain but grows in the wood slowly and causes no greater damage. *O. floccosum* n. sp., with a *Graphium* conidial stage, occurs sporadically in old tunnels of various bark beetles and on mechanically injured stems of pine and spruce. It causes a slight blue stain. *O. clavatum* n. sp. is associated with *Ips acuminatus* on top-logs of pine. This fungus is very common in Sweden and produces a fast developing deep blue stain. Its perithecia are often imbedded in wood, with their necks only reaching into the tunnels. In the imperfect stage it produces numerous ramified graphia with clavate heads. *O. tetropii* n. sp., with small hyaline *Scopularia*-like conidial stage and fast growing slightly pigmented mycelium, is found in the tunnels of the wood-boring beetle *Tetropium* sp. on spruce. In timber, the mycelium spreads only around the tunnels and causes a slight blue-green stain.

Forstliche Versuchsanstalt Schwedens
Experimentalfältet.

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PALYNOLOGY. ASPECTS AND PROSPECTS. II.

EDITED BY

G. ERDTMAN.

The first issue of »Palynology. Aspects and Prospects» was printed in this Journal vol. 42 (p. 467—483), 1948. The second part, herewith published, contains the following contributions:

1. Erdtman y Gamerro: Palinología en Sudamerica.
2. Klaus: Tertiär-Palynologie in Österreich.
3. Sears: Palynology in North America.
4. Sen: Some aspects of palynological research in India.
5. Wetzel: Die Mikropaläontologie des baltischen Kreide-Feuersteins, auch eine Angelegenheit der modernen Paläobotanik.
6. van Zinderen Bakker: Palynology in South Africa.

The contributions 3, 5, and 6 were on the program of the palynological conference held at Bromma as part of the VII. International Botanical Congress, Stockholm 1950.

Erdtman, G. (Estocolmo) y Gamerro, Juan C. (La Plata): Palinología en Sudamerica.

El objeto de esta nota es la de contribuir a la formación de una sólida base para la investigación y colaboración internacional en esta clase de estudios. La bibliografía se encuentra catalogada en 'Literature on Palynology' I a XIV, publicados por G. Erdtman en 'Geologiska Föreningens Förhandlingar', 1927—1951, Estocolmo; no es completa y se ha dado preferencia a los trabajos de autores sudamericanos.

Morfología de Polen y Esporas.

1) Método y teoría. — Labouriau (1947) estudia los rasgos morfológicos de la exina y aplica también la técnica de los rayos X

al estudio de su estructura (LABOURIAU 1947, 1948; LABOURIAU y CARDOSO 1948; LABOURIAU y RAVELLO 1949).

2) Morfología. — Diferentes clases de granos de polen de plantas sudamericanas, han sido descriptos por WODEHOUSE (1935) y ERDTMAN (1943). La obra de G. ERDTMAN 'Pollen Morphology and Plant Taxonomy' a publicarse próximamente contendrá abundante material de polen y esporas de estas plantas. Las siguientes familias y órdenes han sido tratadas en diversas publicaciones: *Acanthaceae* (BRIDAROLLI 1948; el mismo autor tiene un trabajo sobre Acantaceas Bonaerenses a publicarse en el Museo de La Plata; BREMEKAMP 1947, LILLO 1937, RIZZINI 1946, 1947, 1948, 1949), *Bignoniaceae* (GOMES 1949), *Canellaceae* (ERDTMAN 1946), *Compositae* (CABRERA 1944, CORRADI 1940, WODEHOUSE (1928, 1929), *Coniferae* (VAN CAMPO-DUPLAN 1950), *Convolvulaceae (Merremia;* O'DONELL 1939), *Dialypetalanthaceae* (RIZZINI y OCCHIONE 1949), *Diclidantheraceae* (ERDTMAN 1944, O'DONELL 1941), *Eucryphiaceae* (ERDTMAN 1946), *Euphorbiaceae* (*Chiropetalum;* SKOTTSBERG 1949), *Fagaceae* (CRANWELL 1939), *Halophytaceae* (SORIANO 1946), *Isoetaceae* (PASTORE 1936), *Lemnaceae* (GIARDELLI 1937, 1939), *Lycopodiaceae* (KNOX 1950), *Martyniaceae* (*Ibicella* y *Craniolaria;* ABBIATTI 1939), *Ophioglossaceae* (LICHTENSTEIN 1944), *Rubiaceae* (*Randia;* FAGERLIND 1942), *Santalaceae* (DAWSON 1944; *Arjona,* SKOTTSBERG 1940; SWAMY 1950), *Schizaeales* (REED 1947, SELLING 1947), *Thurniaceae* (ERDTMAN 1944), *Zygophyllaceae* (DESCOLE, O'DONELL y LOURTEIG 1939), *Winteraceae* (BAILEY y NAST 1943, 1945).

G. ERDTMAN ha relizado un estudio especial del polen de *Bromeliaceae,* basado especialmente en material coleccionado en Brasil por el Sr. MULFORD FOSTER, Orlando, Florida. U. S. A., cuyos resultados no han sido aún publicados. J. C. GAMERRO tiene en preparación un trabajo sobre morfología del polen en las *Mutisieae (Compositae).*

Es de esperar un mayor incremento de estos estudios entre los investigadores de América del Sur; son numerosas las familias y géneros cuyo estudio del polen podrá proporcionar datos de interés sobre sus relaciones filogenéticas, o un medio para su división sistemática.

Las *Loasaceae, Calyceraceae, Ochnaceae, Quiinaceae, Columelliaceae,* los géneros *Lacistema, Batis, Gunnera, Lissocarpa, Befaria, Philesia* y otros, se hallan entre los que pueden proporcionar excelente material de estudio. Un catálogo de los granos de polen de

especies sudamericanas, citando las obras donde se encuentran descriptos, resultará de mucha utilidad, por tratarse de una disciplina que comienza a dar sus primeros pasos en esa parte del Mundo.

Aerobiología y Polinosis.

Debido a su mayor importancia social inmediata, este aspecto de la Palinología, ha sido tratado con bastante amplitud, existiendo en casi todos los paises servicios organizados para la investigación y tratamiento de las enfermedades alérgicas, pero haría falta no obstante, una estrecha colaboración entre médicos y botánicos para llevar a cabo estudios regionales, única forma de llegar al conocimiento cabal de la flora alergógena de un país. Varios son los institutos dedicados a estos estudios, pudiéndose citar entre ellos: Servicio Alérgico del Laboratorio Carlos Chagas, Belo Horizonte, Brasil; Policlínicos de Alergia de los Hospitales Arrarián y San Vicente, Santiago, Chile; Servicio de Alergia del Dto. de Sanidad, Asunción, Paraguay; Sociedad Brasileña de Alergia, Rio de Janeiro, Brasil; Sociedad Peruana de Alergia, Lima, Perú; Centro de Alergia del Hospital Nacional de Clínicas, Servicios de Alergia de los Hospitales Ramos Mejías, Rivadavia, Militar Central, de la Academia Nacional de Medicina; Instituto Nacional de Enfermedades Alérgicas, todos de Buenos Aires, Argentina. Este último instituto está realizando estudios aerobiológicos por medio de aviones en diversos lugares del país, con miras a la confección de un mapa de las zonas polínicas.

Farmacognosia.

El origen y adulteración de las mieles y de ciertas drogas puede determinarse por medio de su análasis polínico y es una cuestión de importancia económica y legal (cf. Fernandez y Burgues 1943).

Analisis de Polen y Esporas.

1) Depósitos pre-Cuaternarios. — Halle (1940) ha descripto esporas de *Lygodium* de la cuenca carbonífera de Coronel (Concepción, Chile). Thieragrt (1940) halló granos de polen 'tiliodes' en estratos Terciarios (ó del Cretácico superior?) de Brasil, que fueron determinados como afines a las *Bombacaceae* por Erdtman (1944).

En capas Terciarias del norte de América del Sur se han encontrado granos de polen de *Caryocaraceae* y *Olacaceae-Anacoloseae* (ERDTMAN, inédito).

Fuertemente adheridos a la epidermis de *Johnstonia coriacea*, H. A. ORLANDO, encontró en capas Triásicas ('Estratos de Cacheuta', Mendoza, Argentina), un grano de polen alado con cierto parecido a los de *Pteruchus* y *Caytonanthus*, y otros tipos de granos que asimila a las *Pteridospermae*, uno de los cuales parece corresponder a *Antholitus Zeilleri* (a publicarse).

2) Depósitos Cuaternarios. – Los primeros diagramas de polen (de cerca del Lago Fagnano, Tierra del Fuego) fueron publicados por L. von POST (1930, y más tarde en 1946). Posteriores contribuciones han sido las de SALMI (1941) y especialmente V. AUER (1933, 41, 46, 48, 49, 50).

Dentro de las angiospermas sudamericanas encontramos muchos de los miembros más primitivos de familias ampliamente distribuidas, como así también gran número de éstas con área restringida a ese territorio, aparte de otras que comparte con Africa y la región australiana.

Esto puede darnos una idea de la importancia que supone el estudio de su flora actual y fósil (y la de las demás regiones del extinguido Gondwana?), para avanzar hacia el conocimiento taxonómico y filogenético de las angiospermas.

Varias regiones de América austral permanecen todavía inexploradas, especialmente en los trópicos. Sin embargo son muchos los naturalistas que la han visitado coleccionando gran cantidad de material que se halla al alcance de los palinólogos en herbarios de diversas instituciones del Mundo.

El conocimiento del polen de las plantas vivientes es también indispensable para los estudios del polen fósil. Los análisis de las turberas del extremo austral de la Argentina y Chile han dado buenos resultados, y es posible que las Islas Malvinas guarden en sus turbas, la historia de la flora y del tipo de vegetación que las cubría en tiempos postglaciales, pues en toda esa zona la vegetación es propicia para tales estudios.

El resto del territorio no parece ofrecer las mismas ventajas por su vegetación floristicamente heterogenea y casi desprovista de árboles anemófilos.

Sin embargo, sólo el análisis de los distintos tipos de turbas (en

la cuenca del Amazonas y Orinoco, zonas montañosas del Brasil, Uruguay, los Andes y otras), podrá dar la última palabra en tal sentido.

El polen y esporas contenidos en los carbones y sedimentos petroliferos, permitirá tal vez su correlación estratigráfica y determinar las condiciones bajo las cuales se formaron.

Como vemos el campo de acción de la Palinología en América del Sur es muy amplio, y lo será aún más cuando nuevas regiones sean liberadas biológica, geológica y paleontológicamente.

Klaus, W. (Wien): Tertiär-Palynologie in Österreich.

Zur geologischen Erforschung von Tertiärsedimenten wird heute besonders in Erdöl- und Braunkohlengebieten die Mikropaläontologie in erhöhtem Masse herangezogen. Vielfach liegen Probleme vor, welche nach neuen Methoden verlangen. Die Forschungsarbeiten konnten dank der Unterstützung von Frau Prof. Dr. E. Hofmann, Herrn Doz. Dr. A. Papp, Ass. Dr. E. Thenius und der Förderung seitens der Geologen der Kohlenholding G. m. b. H. und Rohöl-Gew. A. G. trotz der zeitbedingten schwierigen Arbeitsbedingungen am Paläontologischen Institut der Universität Wien in Angriff genommen werden.

Der hier neuen Arbeitsrichtung sind etwa folgende Ziele gesetzt:

1. Erweiterung unserer Kenntnisse über die bisher bekannte Tertiär-Flora. Erforschung der Florengemeinschaften sowohl innerhalb der einzelnen Tertiärabschnitte als auch in den synchronen, regional geschiedenen Sedimentationsräumen. —

2. Feststellung aller Pollen- und Sporenformen des Tertiärs im Bereich der Ostalpen. Anbahnung von Vergleichsmöglichkeiten zu rezenten Formen und solchen, welche aus eindeutig bestimmbaren fossilen, inkohlten Blütenständen gewonnen wurden. —

3. Fixierung charakteristischer Pollen- und Sporenvergesellschaftungen in Schichtgliedern, welche auf Grund geologischer und paläontologischer Befunde altersmässig eindeutig datiert sind. —

4. Untersuchung der Frage: Ob und in welcher Art beeinflusst alpine Tektonik das Pollenbild der Tertiärstufen?

5. Vergleich der Florenveränderungen im Laufe des Tertiärs mit Untersuchungsergebnissen aus Ablagerungen anderer geographischer Breiten (Deutschland, Balkan). —

Ad 1. Bisherige Florenbeschreibungen basieren vielfach auf Funden, welche aus Kohlenbegleitschichten stammen. Kohlenflöze lieferten mit Ausnahme von gelegentlich gut erhaltenen Xyliten nicht gerade häufig bestimmbare pflanzliche Fossilien. In alpin bewegten Kohlenvorkommen sind solche wohl nur als Seltenheit zu erwarten. Nach den bisherigen Erfahrungen ist es in unseren weniger gestörten Braunkohlelagern fast immer möglich fossile Sporen und Pollen in bestimmbarem Zustand zu erhalten. Sorgfältig untersuchte Profile erlauben Rückschlüsse auf Florengemeinschaften der einzelnen Flözbildungsstadien und Klimabedingungen. Pollen stellen in Kohlenflözen oft die einzigen Zeugen der Angiospermenflora dar. Wo die Lagerung durch tektonische Vorgänge gestört ist, scheinen der Methode allerdings gewisse Schranken gesetzt. Dann stellt der mangelhafte Erhaltungszustand einer Bestimmung grosse Schwierigkeiten entgegen. Bisher mussten sich die Untersuchungen des Verf. in solchen Fällen auf die oft zahlreich auftretenden Zwischenmittel beschränken, deren Mikrofossilien in der Regel besser erhalten sind. Wie einleitende Analysen gezeigt haben, finden sich in nahezu allen Tertiärstufen pollen- und sporenführende Sedimente. Es ist in Aussicht genommen, für jeden Abschnitt eine Anzahl geschlossener Profile durchzuarbeiten. Durch Vergleich synchroner Horizonte aus verschiedenen Sedimentationsräumen soll die Abgrenzung von Florenbereichen (Inneralpines Wiener Becken, Inneralpine Talmolasse, Ausseralpine Molasse) ermöglicht werden. —

Ad 2. Die im mitteleuropäischen Tertiär auftretenden Pollen und Sporenformen erscheinen im Wesentlichen bereits von R. Potonié, Thomson, Thiergart u. a. Forschern dargestellt. Aus dem Pannon des Wiener Beckens und dem steirischen Kohlenmiozän dürften sich einige anscheinend neue Sporomorphae hinzufügen lassen. Eine Darstellung der Untersuchungsergebnisse über Taxodieae, Taxaceae und Cupressineae (rezent, fossil aus Blütenständen, fossil aus Braunkohlen und deren Begleitschichten) ist in Vorbereitung. Ferner ist ein Atlas aller Sporomorphae des ostalpinen Tertiärs geplant.

Ad 3. Dank der intensiven geologisch-paläontologischen Forschungstätigkeit der letzten Jahrzehnte liegt über das Pannon des inneralpinen Wiener Beckens eine genaue stratigraphische Gliederung vor. (K. Friedl 1937, R. Janoschek 1951, A. Papp 1948.) Es

war daher naheliegend, die erste Profiluntersuchung in diesem Gebiet durchzuführen. Ausgedehnte Braunkohlenablagerungen (Zillingdorfer Kohlenrevier) boten dazu günstige Gelegenheit. Es ist zu hoffen, dass jene Ablagerungen des steirischen Kohlenmiozäns, welche besonders auf Grund der Säugetier-Faunen eingestuft sind, einen ebenso sicheren Fixpunkt für die geplanten Profiluntersuchungen der inneralpinen Talmolasse abgeben.

Ad 4. Der Gedanke, dass der Pollenniederschlag alpiner, bzw. alpennaher Ablagerungen durch Phasen der Gebirgsbewegung beeinflusst sein könnte, tauchte erstmals bei Profiluntersuchungen des Ober-Pannons im Wiener Becken auf. In einem Horizont des basalen Ober-Pannons von Neufeld (Zone F nach A. Papp 1948) setzt u.a. ein Überwiegen von Pinus silvestroiden Formen gegenüber P. haploxylonoiden Formen ein, begleitet von einem Abies- und Picea-Anstieg. Nach Thiergart 1940 (S. 10) überwiegt im deutschen Jungpliozän die silvestroide *Pinus*-Form. Nach theoretischen Überlegungen wäre dieses Bild in unseren südlicheren Breiten noch höher im Pliozän zu erwarten. Da unsere Ablagerungen aber eindeutig unterpliozänen Alters sind, liegt die Annahme einer alpinen Klimabeeinflussung nahe. Je mehr alpine Grosstektonik Flächen höherer Lagen zur Entstehung brachte, desto grösser wurde das Verbreitungsgebiet jener Pinaceae, welche silvestroide Formen produzierten. Schrittweise lässt sich dies in oberpannonischen Spektren verfolgen. Ähnlicher Art ist die Pinusschwankung des Ober-Sarmat im Wiener Becken. Obwohl im Miozän als auch noch im Mittelpannon P. haploxylonoide Formen überwiegen, lässt das obere Sarmat einen deutlichen Anstieg P. silvestroider Formen, *Abies* und *Picea* erkennen. Man könnte hier an den Einfluss der attischen Phase (Stille) denken. Die Prüfung der Möglichkeit, wieweit die Palynologie das Mass endogener Vorgänge — Hochhebung der Alpen, Tieferlegung der Becken — wiederzuspiegeln vermag, soll hier weiter verfolgt werden. —

Ad 5. Der Rückzug wärmeliebender Tertiärelemente besonders im Laufe des Neogens soll durch Vergleich mit Pollenvergesellschaftungen anderer geographischer Breiten (Deutschland, Balkan) untersucht werden. Sichere Schlussfolgerungen dürften erst nach einer grösseren Zahl von Untersuchungen eindeutig datierter Ablagerungen möglich sein. Es sei erwähnt, dass im Pannon des Wiener Beckens (Unterpolizän) flügellose Coniferenpollen bei weitem vor-

herrschen (ca 72 % der Coniferenpollen) Neben castanopsoiden und engelhardtioiden Formen sind castaneoide Pollen bis zu 6 % vertreten.

Bisherige Untersuchungen:

Inneralpines Wiener Becken. Pannon. Die Untersuchungen setzten 1947 gleichlaufend mit neuen Kohlenschürfen (Neufeld) ein. Stratigraphisch eindeutig als basales Ober-Pannon (Zone F nach A. Papp 1948) eingestuft, zählen sie zu den jüngsten kohleführenden Schichten des österreichischen Tertiärs. Eine Makroflora wurde von Stur 1867 bekanntgemacht. Die palynologischen Ergebnisse wurden vom Verf. 1950 (»Palynologische Untersuchungen an der oberpannonen Braunkohle von Neufeld a. d. L.» — Diss. Phil. Fak. Univ. Wien) zusammengefasst. Zum Vergleich erfolgten Einzeluntersuchungen aus angrenzenden Kohlenlagern und Bohrungen (Pöttsching, Stinkenbrunn, Sollenau). Im Anschluss an die von Berger 1950 gründlich untersuchte Makroflora von Vösendorf bei Wien [Mittelpannon (Zone E nach A. Papp 1948)] wurden Einzelanalysen aus den pflanzenführenden Schichten durchgeführt. Gelegentliche Untersuchungen von sarmatischen Bohrproben sowie tortonen Kohlenbegleitschichten (Grillenberg in Niederösterreich) leiten die palynologischen Miozänuntersuchungen ein. —

Ausseralpine Molasse. Dank der Initiative der Kohlenholding G. m. b. H. Wien, wurden 1950 umfangreichere Untersuchungen einiger Profile aus dem Hausruck- und Salzachkohlengebiet ermöglicht. Eine vorläufige Darstellung der Ergebnisse ist in Vorbereitung.

Inneralpine Talmolasse. Die Untersuchungen sind vorläufig im Stadium orientierender Einzelanalysen aus St. Kathrein a. H., Köflach, Zangtal, Parschlug, Tauchen, Lavanttal und Häring in Tirol.

Geplante Untersuchungen: Wo durch Vorproben eine auswertbare Pollen- und Sporenführung erwiesen ist, soll auf Grund systematischer Profiluntersuchungen der Florenwandel im Laufe des Neogens in Diagrammform festgehalten werden. Anschliessend werden die Kohlenablagerungen von Häring in Tirol, Guttaring in Kärnten, Statzendorf (Niederösterreich) sowie der Sotzka-Schichten Gelegenheit zu weiteren interessanten Untersuchungen geben. —

Im Raume der Ostalpen sind die ersten Schritte zur palyno-

logischen Erforschung von Tertiärsedimenten getan. Im Verein mit weiteren Disziplinen der Mikropaläobotanik scheint sie in hohem Masse geeignet, unsere Kenntnisse über Flora, Klima und Geologie des Tertiärs zu erweitern. —

Sears, Paul B. (Department of Conservation, Yale University, Newhaven, Conn.): Palynology in North America.

The first paper on pollen analysis in the United States was published by Draper (1928). The first to be published on Canadian bogs was by Auer (1927), and the first report of pollen spectra in Mexico was by Deevey (1944). Earlier, reviews of European work had been published in the Botanical Gazette by Fuller (1927).

Because of the extent of North America and the small number of workers, there is, as yet, no such precise analysis of glacial and post-glacial history as that available for the Baltic area and the Alps in Europe. However, the history of the Great Lakes has been worked out in considerable detail, and substantial progress has been made in establishing the main events of glacial retreat.

There exists in North America no barrier to the southward migration of vegetation during the advance of the ice. As a result, the postglacial forest flora is far richer than it is in Europe, and there is an extensive peri-glacial area extending into Central America. Although interest has been concentrated on establishing the general sequence of vegetation history, there exists a specific problem based on floristic studies by Gleason (1909) and others. These studies suggested that there had been in postglacial time a climatic period warmer and drier than the present. This is called the Xerothermic period, and one of the first problems of pollen analysis has been to confirm or disprove its existence (Sears 1942).

Because of the wide extent and varied character of vegetation in North America, generalizations have been difficult and slow. One of the most serious initial problems was that of pollen identification, a field in which there was no literature. A number of workers have dealt with the problem of pollen taxonomy, the most thorough study being that of Wodehouse (1935). At the present time little difficulty is encountered in generic determinations, and considerable advancement has been made, especially in the case of *Pinus*, in the determination of specific forms by size-frequency data (Cain and Cain 1948, Hansen 1947).

Diversity of techniques and relative isolation of workers have delayed the standardization of technical methods; for example in the preparation of material and the presentation of results. In general the use of bar diagrams has commended itself because of the rather large number of forms dealt with. The recent extension of studies to unglaciated areas where there is no peat has complicated the problem of preparing samples for study. Interpretation has been rendered difficult not only by the large number of genera encountered but also by the wide diversity of climatic conditions. Thus, for example, oak, which is normally an indication of xerophytic conditions, becomes the opposite in the basin of Mexico, where that genus occupies situations relatively more humid than those occupied by pine.

In extreme habitats, such as the humid Puget Sound area studied by HANSEN (1947) and the dry prairie margin of the interior, which was studied by VOSS (1944), fluctuations in climate appear to be masked. There has been considerable difference of opinion as to the number and meaning of climatic alternations. The greater majority of profiles studied show clearly enough the process of gradual warming to a maximum and subsequent reversal in recent times. However, it is now clear that the farther one proceeds from former glacial centers, the larger the number of alternations between periods which are warm or dry, or both, and periods which are cool or moist, or both (SEARS 1948, WILSON ms.).

The recent summary of glacial retreat by FLINT and others (1945) appears to afford a convenient means of reconciling these facts. It is now known that beginning with the Tazewell and continuing to the present there have been at least six substages, each marked by advance and retreat. Thus the great Wisconsin retreat has been pulsating in character. Within the glaciated area no basin has been found which contains a complete record of all of these changes. The earlier phases are missing. Whether this is due to the long lingering of ice in the sedimentary basins or to some other cause is not yet clear. However, studies now under way by the writer in northern New Mexico and in the central basin of Mexico show an adequate number of such alternations and apparently extend back to an earlier period than the late Wisconsin. This finding is of interest not only because it strengthens the hypothesis that periods of glacial retreat and advance were accompanied by climatic changes sufficient to influence vegetation but is also of great importance in

indicating that such changes are of much wider extent than the area glaciated. This suggests some former climatic controls which were very general. As supporting evidence we now have sedimentary studies within the Gulf of Mexico (Trask, Phleger and Stetson 1947) and in the southern Pacific Ocean.

Some work has been done on interglacial spectra, for example by Lane (1941) in Iowa where Kay's critical studies of Pleistocene horizons have been available. Considerable work has also been done on pre-Pleistocene pollen and other spores.

In an important paper now ready for the press Wilson demonstrates the importance of composite micropaleontological studies which include all possible groups of organic remains in addition to spores and pollen. Used in Tertiary rock analyses such studies can lead to a relatively clear understanding of paleobiological conditions. Wilson is also reporting the results of channel spectra from each of the three main late-Wisconsin drifts. By aggregating the analyses from all layers of a given boring he obtains a total composition characteristic of the respective drift, useful alike in identifying sedimentary columns of unknown provenance and in tracing the varying climatic conditions of glacial retreat.

Less progress has been made in archeological applications than in Eurasia. This is due partly to the relatively sparse pre-European population of North America; also to the absence of peat cutting for fuel. An interesting cooperative enterprise has been the analysis of sediments at the Boylston Street Fishweir in Boston (Benninghoff 1943) which led to the approximate dating of this pre-historic site. At Lake Klamath in Oregon the coexistence of early man with late Pleistocene camel, horse, and elephant has been established (Hansen 1942).

Studies by the writer in the central basin of Mexico, as yet unpublished, have been extremely fruitful in demonstrating that two great waves of culture, the Archaic and the Aztec, were correlated with relatively humid conditions, while the long interval that separated them was relatively dry.

Although the signs of Pleistocene mammals are relatively abundant in North America, pollen analysis has not yet been utilized to advantage in dating these remains because of the unfortunate and seemingly incurable habit of scrubbing bones off immediately after they are recovered. Consequently, the associated sediments are seldom available by the time the discovery is announced.

Perhaps the most impressive regional monograph based on pollen analysis is that of HANSEN (1947) in the Pacific Northwest. Here, as in Mexico, volcanic ash is available as a stratigraphic marker. The forest history has been complicated and made further so by the recurrence of fire and other local disturbances. However, in general HANSEN has uncovered a series of alternations parallel to the later part of the postglacial record farther east. Some confusion has arisen because of disagreement as to the time period involved, which has led HANSEN to support VON POST's simple hypothesis rather than the more elaborate theory of repeated glacial retreats and advances. These questions of absolute time intervals should be solved before too long since at least two laboratories, one at Chicago and one in the University of Michigan, are now equipped to carry on Carbon 14 analysis of organic matter. This makes possible accurate dating of material not more than 35 000 years old.

In the field of geomorphology an increasing number of applications are being made. This includes the correlation with volcanic activity already mentioned. It also includes correlation with lake levels and buried soils in Mexico. In the North Carolina area pollen analysis is being applied to the solution of the peculiar problem of the Carolina Bays (BUELL 1946, FREY ms.). These bays are curious oval lakes with long axes at right angles to be present coast. Their origin has been a subject of considerable debate and various explanations have been advanced as to their nature, including the action of meteor showers. Pollen analysis will presently reveal whether these lakes are all of the same age or have originated in different times.

This report would not be complete without some mention of the numerous studies of POTZGER (e.g. 1948 a and b), which extend from Maine and Southern Canada to Texas. POTZGER has been extremely conservative in drawing inference as to climatic change, but a recent examination of his reports reveal nothing seriously inconsistent with findings elsewhere.

One of the lively problems in American climatic history is the extent to which northern vegetation was displaced during glaciation. POTZGER and THARP (1947) have reported Canadian conifers in Texas, CAIN (1944) in South Carolina, and WILSON (1946) in Florida. These reports are supported by BROWN's (1944) findings of macrofossils in Louisiana and by HANNA's (1933) earlier report of northern diatoms toward the base of Florida peat deposits.

Among the technical problems now receiving attention are refinements of pollen classification, notably the studies of CAIN, HANSEN, and others on pine already referred to. CAIN has in preparation an extensive atlas of pollen, WILSON an iconographia of over 12 000 photomicrographs of fossil spores and pollen from Devonian to Recent sediments. Other technical problems include the analysis of mineral sediments containing pollen, a process which appears to be complicated by the mineralization of the pollen itself and by the great chemical variation of the sediments. The buoyancy of various kinds of pollen and its effect on pollen spectra is likewise receiving attention (HOPKINS ms.).

Acknowledgement should be made to the influence of Dr. ERDTMAN's visit to the United States in 1931, during the course of which he not only called attention to certain difficulties to be met in Canadian peat deposits, but gave to botanists in several institutions the benefit of his counsel. In general, it may be stated that satisfactory progress is being made not only in improvement of technique and the accumulation of data but in the vital collaboration between pollen analysts and workers in cognate fields.

Informal communication has been maintained among palynologists since 1943 by means of the Pollen Analysis Circular. Sponsored by the Oberlin College Herbarium, it is at present edited by L. R. WILSON, University of Massaschusetts, Amherst, Mass., and PAUL B. SEARS, Department of Conservation, Yale University, New Haven, Conn. Assistance in mimeographing and mailing has come from numerous co-workers. This circular, which appears at irregular intervals, is now in its 17th number and has a mailing list of about 180 workers in various parts of the world.

The bibliography for North American palynology now amounts to some three hundred papers. Obviously much that is of importance and interest must be omitted in a brief report such as the foregoing.

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Sen, J. (Botanical Laboratory, University College of Science, Calcutta): Some aspects of palynological research in India.

Since the publication of the Late Professor Birbal Sahni's article on the prospects of palynology in India, which appeared in this journal about two years ago, it has been felt necessary to review the attainments and problems of the Indian workers in this field as a useful supplement to his excellent account.

For some years now, workers in India are gradually developing interest in the wealth of spores and pollen entombed in coal, especially because of their decisive role in the correlation of coal seams and similar rock systems. These organic links have a direct bearing on the efforts of coal-hunting geologists, who by the application of this new knowledge have stumbled upon new discoveries in otherwise unsuspected areas.

Since the appearance, about six years ago, of the first note on the microfloral correlations of a number of productive coal seams in the disturbed eastern portion of the Indian Upper Coal Measures, attempts of this kind have been shy so far as the Southern Hemisphere is concerned. Even so, the knowledge acquired through the study of the rich spore flora of the Lower Gondwana coal in India has been profitably utilised for local correlation work in the Raniganj and Karharbari coal fields, and such possibilities are now being explored at Bokaro. Lately some work has been done to evaluate the nature of coal from microfossil analysis of some palaeozoic and tertiary seams, and the results so far obtained are full of promise and pregnant with useful information.

It may be recalled that a few fronds of the *Glossopteris* have led to the opening up of the productive Coal Measures in South Rewa, near Upper Umaria. Similar discovery of characteristic Lower Gondwana spores and pollen (otherwise recognised as the *Pityosporites* flora after the name of the dominant *Pityosporites* type of pollen in the microflora) in localities barren of megafossils may prove useful in guiding explorations. The facts at hand certainly justify such possibilities.

The numerous species of microspores of the Indian palaeozoic coals now recognised as constituting a *Pityosporites* flora is highly characteristic throughout the Gondwanas. This has widened our ideas of the *Glossopteris* (? = *Pityosporites*) flora and its relation

to the floras of the North. It is becoming more real than apparent that our coal flora is not altogether different from the contemporaneous Northern flora — such a possibility was first suggested on independent grounds about thirty years ago by the Late Professors SEWARD and SAHNI.

In India the most persistent problem in coal seam analysis is the classification of the 'spore types'. What seems immediately necessary is the evolution of a suitable system which may help to correlate the spore data of different authors for interregional and similar correlations.

The current systems of classification for the spores of the Northern Coal Measures are either morphologic or based on proper taxonomic principles. The morphologic systems are often locally useful, but not otherwise reliable. It may also be difficult to place all of our 'spore types' suitably under the genera emerging from the essentially botanical and taxonomic systems of SCHOPF *et al.* and others. Provisionally a morphologic system following the nomenclatural principles of RAISTRICK is now being followed in this country.

The drift origin of our coal seams, their structure — often considerably thick at some places and splitted and fragmented at others, their low volatile contents, and the probable presence of assumed developmental stages of the same species of spore (as demonstrated to be present in the British coal by Dr. LESLIE MOORE) are among the many problems that the workers here are facing. While some of these factors have been partially overcome, the majority of the problems still remain to be solved.

Palynology has played a decisive role in settling many disputed problems of dating our apparently unfossiliferous rocks. For example, the discovery of angiospermous remains and spores and pollen in the famous Saline Series has adduced evidences in favour of its tertiary origin quite in contradiction to the belief of some eminent geologists who assigned its date anachronistically back into the remote cambrian. Since then the Saline Series has been a fascinating study for both the botanists and the geologists alike. Examination of control rock samples from the undisputed cambrian beds overlying the Saline Series and from other parts of India has revealed the possibility of the existence of a vascular flora, not angiosperms however, deep down in the cambrian. This work is now being continued at several laboratories in this country and the re-

sults of such investigations may have far reaching effects in our concepts of the origin of vascular plants.

The occurrence of pollen flora part of which is referable to modern genera of angiosperms has provisionally settled the disputed age of the Cherra sandstones (tertiary) and added more evidences in favour of a tertiary age for the Deccan Intertrappean beds. Similar attempts are also being made to determine the age problem of the Barmer strata in Rajasthan. It is becoming increasingly evident that our fossil spores and pollen have wider prospects for dating the sedimentary deposits of unknown and disputed age, and various pre-carboniferous formations in many parts of India, specially those yielding or likely to yield deposits of economic importance. But the identification of most of the spore and pollen species recovered from the younger rocks has been found to be very difficult due to the absence of 'a standard collection of modern spores and pollen', and the situation has not since improved.

Sanders in England has attempted to evaluate the significance of the microscopical observations of crude petroleum and their bearing on the problems related to the genesis of oil, as well as the possibility of utilising the microbotanical method for correlation purposes connected with the correlation of oils with reservoir formations or source deposits, and indirectly with questions of stratigraphical geology. Oil prospecting in India has created a renewed interest among the palynologists. The tertiary successions in Assam have been partly correlated in search of oil bearing horizons, but a wider field as outlined by Sanders is yet to be explored.

I have presented very briefly some of our attainments and problems, and the necessity and scope of development of palynological research in India. I feel our colleagues in different parts of the world will understand our points of view and the situation we are facing here.

Wetzel, O. (Eutin, Holstein): Die Mikropaläontologie des Baltischen Kreide-Feuersteins, auch eine Angelegenheit der modernen Paläobotanik.

In gelegentlichen Dünnschliffen und den splitterartigen Bruchstücken, die nach der Methode von Walter Wetzel aus den zerschlagenen Flintknollen gewonnen wurden, spielen neben den tierischen auch die pflanzlichen Reste des Kreidemeeres eine er-

hebliche Rolle, und zwar vor allem die Algen des Planktons. Ihre geologische Überlieferung beruht weniger auf der primären Absonderung von mineralischen, harten Schalen oder Gerüsten als auf dem Vorhandensein organisch-chemischer Zellwände, die wir als weicher auffassen und Hüllen nennen. So sind die Kalkplatten der *Coccolithophorideae*, einer pflanzlichen Flagellaten-Gruppe, welche vorwiegend den Kreide-Schlamm zusammensetzt, wegen ihrer Kleinheit und diagenetischem Vergänglichkeit mir nie im baltischen Feuerstein begegnet. Dasselbe gilt für die besonders winzigen Kieselgerüste der *Silicoflagellideae*. Diese und noch mehr die Kieselschalen der Diatomeen, die Kieselgerüste der Radiolarien und die Skelettnadeln der Kieselspongien haben gerade durch ihre Auflösung einen wesentlichen Beitrag zur Bildung des Feuersteins geleistet. Spongien-Reste sind freilich von gröberer Natur und häufig noch im Flintsplitter zu sehen, Radiolarien seltener.

Zum ersten Mal fand ich neuerdings im baltischen Flintstein mehr oder minder deutliche Reste von Diatomeen, deren zarte Kieselschalen selbst in dem baltischen Kreidekalk nur selten sind. Als sicher darf wenigstens die Deutung einer Kette von dunklen, an den Ecken gehörnten Zellen gelten, die wohl von einer der sehr variablen *Hemiaulus*-Arten des Kreidemeeres stammt. Unsicherer ist die Einordnung eines kleinen scheibenförmigen, mit 13 Strahlen versehenen Körpers, der sich in einem grossen Dünnschliff eines noch an Kalkeinschlüssen reichen Danien-Flintsteins befindet und selbst kalkinkrustiert ist. Formell besteht eine Ähnlichkeit mit gewissen Schalen von Asterolamprinen, wie etwa *Asterolampra* Weissflog 1880 oder *Actinoclava* O. Müller 1912.

Reichlicher und mannigfaltiger sind die auf organisch-chemischer Grundlage gebildeten Hüllen, deren Träger vorwiegend als Flagellaten aufgefasst werden. Zuerst sei ein Vertreter der Chrysophyceae, spez. der Chrysomonadeae, genannt: *Dinobryon* cf. *balticum*, eine baumförmig verzweigte Kolonie von trichterförmigen Hüllen, deren Erbauer vermutlich, wie das rezente *D. balticum*, planktonisch oder pseudoplanktonisch, z. T. im Brackwasser, lebten.

Zu den Desmokontae unter den Algen rechnet George Deflandre, nach dessen Systematik der fossilen Flagellaten ich mich hier richte, unsre seltsamsten Mikro-Funde im Feuerstein, meinen *Ophiobolus lapidaris* und seinen *Dimastigobolus longifilum*, die er als *Ophiobolaceen* zusammenfasst. Es sind ca. 20—40 Mikron

grosse, ovale, häutige Zellen, die noch als schätzungsweise 60 Millionen Jahre alte Fossilen im Flintsplitter wohlerhaltene, z. T. sehr lange Geisselfäden tragen. Dies Ergebnis unsrer Beobachtungen zeugt von einer selten günstigen Erhaltungsmöglichkeit, welche der ursprünglich gelartige Flintstein selbst sehr empfindlichen Zellorganen bot, und weiter von einer relativ schnellen Bildung des einschliessenden Kieselminerals.

Der grösste Teil der fossilen Flagellaten wird den heutigen Dinophyceae angegliedert mit den Untergruppen Dinoflagellatae und Hystrichosphaerideae. Unter den Dinoflagellatae zeichnet sich eine kleine Familie *(Gymnosclerotaceae)* durch den Besitz eines Innenskeletts aus. Als Reste solcher merkwürdigen Innenkörper sehe ich die beiden fünfstrahligen, dunklen Sternchen von ca. 70 Mikron Durchmesser an, die ich in zwei verschiedenen Feuersteinen fand *(Cymnodinium pentasterias)*.

Im allgemeinen herrscht bei den fossilen Flagellaten des Feuersteins eine *Peridinium*-Form als Typ vor. Freilich ist das Plattenmuster ihres Panzers, das für die heutige Systematik so wichtig ist, bei den Feuerstein-Fossilien nur sehr selten zu entziffern. Eine Ausnahme bildet das dem rezenten *Peridinium conicum* (Gran) Ostenfeld & Schmidt identische Exemplar, das George Deflandre in einem Danien-Feuerstein feststellte. Mit diesem *Peridinium* nahe verwandt und vielleicht oft verwechselt ist das *Palaeo-Peridinium pyrophorum*. Genauer untersucht von Mme M. Lejeune-Carpentier in Lüttich wurden weitere Arten, wie *Pal.-Per. galeatum* und *tricuspis*. Seltener sind Vertreter der Gattungen *Gonyaulax* und *Ceratium* (bzw. *Palaeo-Ceratium*) vertreten. Einmalig und von abweichender Gestalt ist der Dinoflagellat eines Senon-Feuersteins, den ich mit dem rezenten *Polykrikos* verglich, der auch aus einer kurzen Kette peridineenhafter Zellen besteht. G. Deflandre hat meinen Fund später näher untersucht und als *Wetzelodinium tentaculatum* neu beschrieben.

Die zweite Unter-Gruppe der Dinophyceae im System der fossilen Algen nach G. Deflandre bilden die *Hystrichosphaerideae*. Diese sind im typischen Falle kleine, sphaeroidale Hüllen mit stachelartigen, an ihrem Ende oft verzweigten Hautfortsätzen. Unser Altmeister der Mikro-Geologie C. G. Ehrenberg beobachtete sie schon vor gut 100 Jahren in Geschiebefeuersteinen. Er hielt sie für Verwandte der Zygosporen gewisser Conjugaten-Algen, die heute jedoch nur im Süsswasser leben. Seine sog. »Xanthidien» wurden um 1905

von zoologischer Seite umgedeutet zu Verwandten der rezenten »Stacheleier» von marinen Planktonkrebsen (Copepoden). Da auch diese systematische Einordnung der fossilen Stachelhüllen (durch H. LOHMANN) nicht befriedigte, habe ich für sie im Jahre 1932 bzw. 1933 eine neue Gruppe aufgestellt mit dem Familien-Namen »*Hystrichosphaeridae*». Später hat A. EISENACK sie zur Ordnung der *Hystrichosphaerideae* erweitert und einen grossen Teil seiner silurischen »Stachelzysten» und vermeintlichen »Ova hispida» in sie miteinbezogen. Ähnliche Mikrofossilien hatte in Nordamerika schon M. C. WHITE 1862 in paläozoischen Gesteinen gefunden. Andererseits kommen unsre *Hystrichosphaerideae* auch in tertiären und diluvialen Sedimenten vor, in den letzteren vielleicht z. T. erst durch Umlagerung von geologisch älterem Material. In den heutigen Meeren scheinen die vermutlichen Nachkommen unsrer kretazeischen und tertiären »Stachelhüllen» ihre hervorragende Rolle in der Zusammensetzung des Meeresplanktons an die typischen Peridineen abgetreten zu haben. Doch sind sie stellenweise nicht ganz selten in den Netzfängen der Planktonfischerei enthalten. Manchmal findet sich sogar die typische Ausbildung einer grossfeldrigen »Täfelung» auf ihrer Oberfläche, wie sie insbesondere der von C. G. EHRENBERG aufgestellten Kreideform *Hystrichosphaera furcata* zukommt.

Dieser Art schliesst sich die von mir beschriebene, mit besonders kräftigen Fortsätzen versehene *Hystrichosphaera cornigera* an. Weitere Gattungen sind z. B. das *Hystrichosphaeridium* (nach G. DEFLANDRE), die *Areoligera* (nach M. LEJEUNE-CARPENTIER), ferner die zierliche *Cannosphaeropsis*, die ein radiolarienähnliches Gitterwerk auf einer Zentralblase trägt, die *Membranilarnax*, deren Stachelkleid von einer Aussenhaut umgeben ist, die *Triblastula* mit ihrer eigenartigen Dreiteiligkeit und die *Cymatiosphaera*, ein Sphaeroid, das ähnlich wie die *Hystrichosphaera* gefeldert, jedoch unbestachelt ist.

Ausser den zuletzt genannten Vertretern, die noch zu den flagellatenhaften Hystrichosphaerideen gerechnet werden, gibt es bei unsern mikropaläontologischen Untersuchungen noch manche andere stachellosen Hüllen im Feuerstein, und hier wird die Deutung noch schwieriger als schon bei den bestachelten Formen. Auf beide, die bestachelten wie die unbestachelten Mikrohüllen, die übrigens im Gestein oft aufgeplatzt oder beschädigt sind, sollte der moderne Paläo-Botaniker besonders achten.

Denn, wie ich schon in meiner Dissertation v. J. 1933 näher aus-

führte, erzeugt nicht nur das Protistenreich, sondern auch die Metazoenwelt und die Festlandsflora eine Menge ähnlicher Kleinformen als Vermehrungskörper etc. Insbesondere kommen Sporen- und Pollenkörner grösserer Landpflanzen hier in Frage. Auch in den Zeiten der entfernteren geologischen Vergangenheit sind sicher Wolken solchen Pflanzen-»Staubes» weithin auf das Meer verweht, und ein Teil der Körner mag sich am Meeresboden abgelagert haben. So wies G. Deflandre wohlerhaltenen Coniferen-Pollen in einem französischen Kreidefeuerstein nach. Rich. Kräusel wies kurz darauf auf die auffallende Ähnlichkeit gewisser Hystrichosphaerideen in A. Eisenack's Silur-Proben mit seinen Sporen-Funden aus dem rheinischen Mitteldevon hin. Entsprechend könnten auch unter meinen kretazeischen Mikro-Hüllen des Feuersteins hier und da »verkappte» Sporen oder Pollenkörner als widerstandsfähige Schalenreste stecken.

Zum Schluss seien nur noch zwei besondere Fälle von rätselhaften Formen erwähnt, weil sie gegebenenfalls auch den Paläo-Botaniker angehen könnten. — Das eine Mikrofossil nannte ich nach der Maulbeere »*Morulosa*», d. h. rundliche Verbände kleiner häutiger Sphaeroide: sind dies etwa sog. Pakete von planktonischen Copepoden-Eiern bzw. Eihüllen oder aber pflanzliche »Cönobien», wie bei den Algen *Coelastrum* oder *Phytomorula*? Zweitens finden sich im Feuerstein verstreut andre Sphaeroide, die meistens einen dunklen Kern und rings herum eine konzentrische, feine »Schichtung» besitzen. Ursprünglich hielt ich sie für Statolithen kleiner Meeresbewohner; neuerdings fand ich solche Gebilde jedoch im Inneren von Polypen-Kammern gewisser Feuerstein-Bryozoen. Einige von ihnen zeigten eine besondere Formung ihres Hüllen-Inhalts, der vermuten lässt, dass es sich hier um verschiedene Entwicklungszustände eines Schmarotzer-Wesens im Bryozoentier handelt. Das wäre wenigstens eine Deutungsmöglichkeit jener zystenartigen Mikrofossilien von etwa Ovoidgestalt. Auch bei solcher Annahme bleibt noch die Frage offen (wie bei den »Morulosae» hier oben): Sind meine »Ovoide» in den Flint-Bryozoen pflanzlichen oder tierischen Ursprungs? Ich selbst denke in erster Linie an eine Zugehörigkeit zu den Flagellaten. Weitere Angaben finden sich in meiner kürzlich im Neuen Jahrbuch für Mineral. etc. erschienenen Abhandlung über neuere Deutungsversuche an Mikro-Formen des baltischen Feuersteins (Abhdl., Bd 91, Abt. B, 1950: 161–192).

van Zinderen Bakker, E. M. (University of the Orange Free State, Bloemfontein): Palynology in South Africa.

Palynological research in South Africa is still in a preliminary stage. During the past three decades only a few papers have been published on this subject. The first contributions to the study of pollen have been in connection with hay-fever. At present the research on pollinosis is carried out in the South African Institute for Medical Research in Johannesburg.

POTTS (1918, 1921, 1922), PIRIE (1928), WATT (1937) and ORDMAN (1945, 1947) have investigated the field of South African »seasonal hay-fever». As a result of their work it is known now that pollinosis in summer is almost invariably due to grass pollen, while winterspring hay-fever may be brought about by *Cupressus*-pollen. *Compositae* and weeds are unimportant etiological pollen factors in South Africa. *Schinus Molle* L. may cause pollinosis under special conditions of heat and drought. For this recearch in allergy counts of atmospheric pollen have been made by POTTS in Bloemfontein and by ORDMAN in Johannesburg.

Long after the work on the medical significance of pollen was started, interest was aroused in pollen morphology and its applications. The first to do work in this direction was GARSIDE (Bolus Herbarium, Cape Town) (1946) who made an extensive study of recent pollen of *Proteaceae,* and *Amaryllidaceae* with related families. His paper on »The Developmental Morphology of the Pollen of *Proteaceae*» is an important contribution to our knowledge of the orientation of the pollen in the tetrad.

The pollen morphology of some important South African families of the Centrospermae, including almost all the very numerous genera of the *Aizoaceae,* was described by Miss LE ROUX (University of Cape Town, 1949).

The writer of the present report has made a collection of pollen samples which represent most of the important genera of South African plants. A slide collection has been started and a pollen atlas is being prepared and will be published in sections. The part on Gymnosperms and Monocotyledons is now ready for publication. This work has been subsidised by the South African Council for Scientific and Industrial Research.

Miss COETZEE (University of the Orange Free State, Bloemfontein) is comparing the pollen types of the various groups of Acacia.

MARTIN (Rhodes University College, Grahamstown) is describing the pollen of the indigenous *Podocarpus* spp. and has made an extensive collection of pollen-slides of all the important plants growing between Port Elizabeth and Cape Town. Mrs LEVYNS (University of Cape Town) is studying the pollen of *Polygalaceae* in connection with her systematic work on this family. FRIEDE (6 Judith Road, Emmarentia, Johannesburg) has also started a collection of indigenous pollen.

To get an impression of the recent pollen deposited on the ground in different types of vegetation, surface soil samples have been collected by the writer of this report in various parts of the Union. In the semiarid warm regions in the interior of the subcontinent, pollen is not likely to be preserved and pollen counts in samples from those parts will probably not give significant results. MARTIN is studying overrepresentation of pollen of certain species in the Knysna forests.

In this connection counts of atmospheric pollen have been made by MARTIN in Grahamstown and by the author in the grassveld area on the outskirts of Bloemfontein.

After the morphology of the South African pollen has been investigated, results may be achieved in pollen analysis. Deposits which are suitable for this purpose are very seldom found in South Africa and therefore research on this line has hardly been done up till now. There are only a few records of fossil pollen found in literature. F. KIRCHHEIMER (1934) investigated the Upper Cretaceous of Banke in Namaqualand in this respect, and E. R. ROUX (1937) gives some information on fossil pollen in black combustible soils of the river valleys of the Witwatersrand.

Now that the writer of the present report has found several isolated peat deposits in various parts of the country it is likely that South Africa may contribute to our knowledge of the history of vegetation and climate. The most important of these peat deposits were found near Cape Town, in the centre of the Orange Free State, in the North of Zululand, near Durban, near the Witwatersrand and in Basutoland. In the deeper layers of some of these sites the peat gradually merged into lignite.

MARTIN is specially studying the lakes in the Knysna area and intends making a map of that region and further to analyse the peat found there. FRIEDE has been investigating the »vleisoils» and the peat of the Witwatersrand in order to get information on the

former vegetation of the high-veld in the Transvaal. He has also done a fair amount of chemical analysis on peat samples.

It is expected that it will be difficult to coordinate the results obtained from the various sites as there does not exist a suitable time scale for the Pleistocene and the Holocene Period in South Africa. For this purpose contact is sought with archaeologists so that their chronology can be calibrated with the palynological findings. It will be a long time before we will obtain an image of the vegetation and climate of the past of South Africa which is as clear as that already existing for Europe.

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SMÄRRE UPPSATSER OCH MEDDELANDEN.

Föreningens medlemmar uppmanas att till denna avdelning insända meddelanden om märkliga växtfynd o. d.

Några bidrag till kännedomen om Stockholmstraktens flora.

Vid en exkursion till Gåsberget (Järfälla sn, Stockholms län), ett av de mera framträdande »botaniska sydbergen» inom länet och beläget ca 3,5 km norr om Hässelby Villastads järnvägsstation, iakttog undertecknad 1947 blommande exemplar av *Phyteuma spicata* L. Beståndet har senare ökat och torde nu omfatta ca 50 individ. Av typiska »gräsmatteinkomlingar» att döma synes det uppenbart att platsen om ock för länge sedan varit under hävd.

Gåsberget hyser en mycket rik och vacker flora, ej minst ur bryologisk och mykologisk synpunkt. Talrika uppgifter om platsens fanerogamflora finnas angivna i Stockholmstraktens Växter (2:a uppl. 1937). Förutom *Phyteuma* har ej heller *Coeloglossum viride* L. tidigare varit känd från Gåsberget.

Från Turebergstrakten kunna följande arter angivas som nya för detta område. *Chenopodium hybridum* — villaträdgård vid Edsviken, förmodligen inkommen genom biohum-gödsel från Henriksdal, Stockholm; *Cirsium heterophyllum* — vid transformatorbyggnad efter Ryavägen; *Geranium pyrenaicum* och *Lactuca serriola* — västra järnvägsbanken söder om Turebergs järnvägsstation; *Impatiens parviflora* — utfyllning av vägkurva Edsviksvägen; *Oenothera biennis* — vid Helenelunds järnvägsstation; och till sist *Oxalis stricta,* som iakttagits i en villaträdgård vid Lillherrsbyvägen. Dessutom har en vitblommig form av *Geranium pratense* observerats i naturreservatet vid Edsviken.

Osw. Sandberg.

Botrytis anthophila (Bond.) funnen på Irland.

Under ett besök på Irland sensommaren 1950 påträffade jag i en klöverodling, tillhörig Albert Agricultural College, Dublin, den 19 aug. parasitsvampen *Botrytis anthophila* (Bond.). Svampen, som är fröburen, åstadkommer en förstöring av frömjölet men anses icke ha någon större betydelse för klöverfröodlingen. Den har tidigare icke anträffats på Irland, men är känd från bl. a. England (Silow: Trans. Brit. Myc. Soc. 1933) och har även påträffats i Sverige (Bergström: Växtskyddsnot. 1940).

B. Wahlin.

RECENSIONER.

Flora SSSR [Flora Sojusa Sovjetskich Socialistitcheskich Respublik] del 1—14 (Pteridophyta—Vitaceae).

Huvudredaktör för delarna 1—13 akademiker V. L. Komarov (delarna 11—13 utgivna efter hans död), för del 14 B. K. Schischkin. — SSSR:s Vetenskapsakademis botaniska Institut, Leningrad 1934—1949; 302 + 778 + 636 + 760 + 762 + 956 + 792 + 696 + 549 + 676 + 432 + 918 + 588 + 790 (= 9635) sidor, 2 kartor. På ryska med latinska diagnoser på nya arter och talrika bilder.

Latinsk titel: Flora URSS [Flora Unionis Republicarum Sovjeticarum Socialisticarum].

De förenade sovjetrepublikernas område omfattar mer än 21 millioner kvadratkilometer eller omkring 1/6 av jordens landyta från Franz Josefs Lands, Novaja Zemljas och Nysibiriska öarnas högarktiska isfält till västra Centralasiens öknar och till Kaukasus', Pamirs, Altais och Ussuris bergskedjor långt nere i den tempererade zonen. Det är givet att ett sådant område skall hysa en rikhaltig och skiftande flora.

Det första försöket att erhålla en översikt över detta ofantliga områdes flora gjordes av Karl Friedrich von Ledebour, professor i Dorpat, som trots betydande motstånd från flera håll lyckades fullborda sin Flora Rossica, tryckt i fyra delar åren 1842—1853, den sista utkommen ett par år efter hans död. Detta arbete, som i precision och konsekvens söker sin like inom den samtida floristiska litteraturen, var ännu när recensenten 1919 först började sina studier av den ryska floran den viktigaste källan till kunskapen om växternas förekomst och utbredning inom det ryska riket. Ledebour uppräknar och beskriver 6568 arter, tillhörande 1139 släkten, i sin Flora Rossica. Artantalet steg raskt på grund av nya upptäckter och på grund av den förändring i artbegreppet mot allt mindre enheter, som gjort och alltjämt gör sig gällande. Ernst Rudolph von Trautvetter tog till sin uppgift att komplettera Ledebours Flora och publicerade åren 1882—1884 sin Incrementa Florae phaenogamae Rossicae (1—4), där ytterligare 6106 arter fogas till de av Ledebour från ryska riket kända. Denna stora ökning beror dock delvis på förändring av det behandlade områdets begränsning.

Det är uppenbart att dessa båda för sin tid utmärkta arbeten ej kunna svara mot modärna fordringar på en Flora. Den botaniska verksamheten har raskt tilltagit, särskilt under 1900-talet, och en mängd viktiga floror behandlande skilda delar av Ryssland ha publicerats. Det kan kanske

räcka att erinra om Fedtschenko & Flerovs flora över Europeiska Ryssland, Majevskis flora över mellersta Ryssland, Kuznetzovs, Lipskis och Grossheims Kaukasusfloror, Fedtschenkos arbeten över Turkestan, Krylovs detaljerade och omfattande Västsibiriens Flora samt Komarovs och recensentens Kamtchatkafloror.

Att återigen sammanföra allt som är känt om det ryska rikets flora till ett enda verk måste framstå som ett jättelikt företag. År 1931 beslöts emellertid att en sådan flora skulle utges. En kommitté fastställde grunddragen i dess uppställning. Det nuvarande Ryssland beräknades hysa omkring 20 000 arter och floraverket beräknades komma att omfatta 15 delar av vilka 1—3 skulle utkomma varje år. Enligt beräkning att blott en del utkom pr år skulle arbetet alltså ha avslutats 1946. År 1949 hade 14 delar utkommit och man hade hunnit fram till familjen *Vitaceae* i Englers system. Antalet behandlade arter var då 9333.

Ungefär 1/3 av systemet återstår alltså att behandla. Antalet band torde därför komma att uppgå till över 20, medan antalet arter kanske stannar något under de beräknade 20 000, ehuru de apomiktiska Compositésläktena avsevärt kan förrycka en sådan beräkning.

De av 1931 års kommitté fastställda grunderna för floran ha blivit normgivande för dess utformning, även om en förskjutning av principerna i vissa fall har ägt rum under arbetets gång. Dessa grunder sammanfattades i 13 punkter, som återfinnas i florans företal. Floran skulle uppställas efter Dalla Torre & Harms, Genera Siphonogarum. Den skulle vara i överensstämmelse med evolutionslärans principer och så vitt möjligt spegla utvecklingen. Såväl släkten som arter skulle tagas i sin minsta vetenskapliga omfattning. Genom denna bestämmelse lyfte kommittén en stor börda från medarbetarna. Dessa behöva ej bekymra sig om att gradera den inbördes släktskapen mellan de typer de behandla. Varje typ skall behandlas som en fristående enhet. Denna analytiska tendens synes för övrigt vara rådande även i andra länder. Försök att samordna mycket närstående typer till naturliga arter i linnéansk mening synas bli allt mindre uppskattade. I Flora SSSR har man dock hållit på, att yttre morfologiska skillnader skall finnas mellan arterna och ej blott inremorfologiska, såsom skillnader i kromosomtal och dylikt.

Nycklar, som finnas till alla släkten, skola vara praktiskt anordnade, alltså artificiella, utan anspråk på att spegla den inbördes släktskapen. Detta är nog nödvändigt, då konstruktionen av användbara nycklar, så idealiska att de ge uttryck åt den naturliga grupperingen, torde stöta på oöverstigliga svårigheter. Alla släkten och arter skola ha en kort karakteristik och släktenas omfattning skall göras så att även andra nu ej kända arter kunna inrymmas i dem. Kritiska anmärkningar skola vara korta, helst ej mer än två rader, och hela behandlingen av en art bör ej överskrida 1200 bokstäver. Varieteter och former upptagas ej som egna enheter men kunna omnämnas i texten med auktorsnamn men utan litteraturhänvisning.

För varje art skall anföras: artnamn, plats för första beskrivningen, synonym, hänvisning till publicerade bilder, exsiccat, ryskt namn, beskrivning på ryska, uppgift på månad för blomning och fruktmognad, växt-

platsens ekologiska karaktär, geografisk areal, typlokal och plats där typen finnes bevarad, samt artens ekonomiska betydelse. Vid angivande av den allmänna utbredningen tas särskilt hänsyn till länderna, som gränsa till Ryssland, medan längre bort belägna länder nämnas summariskt. Inga uppgifter angående närstående arter skall givas.

Hybrider som ha självständig areal upptagas i nyckeln och ha artnummer, andra omnämnas i texten. Alla släkten och arter skola ha ryska namn. I huvudsak skola artnamnen vara binära och svara mot det latinska namnet. De skola dock ej vara en bokstavlig översättning av det latinska namnet, utan böra svara mot växtens natur. Då växten redan har ett stabiliserat ryskt namn (t. ex. i fallen hallon, åkerbär, hjortron, körsbär) skall man dock icke göra binära namn utan nöja sig med dessa folknamn. Man avstår således ifrån att kalla hjortron för hjortron-hallon och åkerbären för åkerbärs-hallon osv. Släkten med begränsad utbredning bör få de namn som de ha i sin hemort. Artnamnen skola alltid stavas med liten bokstav. (Dock stavas artnamn härledda från personnamn med stor bokstav.) Kulturväxter anföras endast om de ha större utbredning eller om de lätt förvildas.

Den kände paleobotanisten A. N. Krischtofovich har givit en fullständig lista på alla tertiära arter, som äro funna inom området, och dessa anföras i floran. Växter från äldre geologiska perioder, som icke ha någon anknytning till den nuvarande floran, anföras däremot ej.

I varje del av floran finnes helsidor med i regel goda tecknade habitus- eller detaljbilder, varierande i antal i de olika delarna mellan 14 och 55.

En utredning om artbegreppet återfinnes i florans inledning. Arterna äro ej likvärdiga, några arter äro mycket beständiga och ha liten variabilitet t. ex. *Iris pseudacorus*, *Acer platanoides* och *Rhododendron chrysanthum*. Komarov anser, att detta beror på att olika agentia ej verka differentierande på dem, vilket nog kan diskuteras. Snarare äro de gamla arter, som fått sitt biotypbestånd reducerat av de påfrestningar de blivit utsatta för genom förändringar av levnadsvillkoren, främst klimatet, under olika perioder. Andra arter, t. ex. *Epilobium angustifolium*, visa stor variabilitet och ha olika lokalraser på många ställen. I Flora SSSR har man valt att betrakta en variationsserie som en serie arter och att inte använda subspecies och varieteter »enär detta bäst svarar mot det praktiska och ekonomiska behovet».

En förskjutning mot ett enligt recensentens mening sundare artbegrepp har dock skett under utgivandet av det stora verket och såvitt jag kunnat finna möter man för första gången i 11:te delen sid. 252 begreppet subspecies, när *Trifolium pratense* subsp. *praecox* Witte överföres till subspecies under *Trifolium sativum*.

Ett par exempel på den oerhörda uppsplittring som blivit följden av det använda artbegreppet kanske borde nämnas. Släktet *Astragalus*, florans största släkte, omfattar hela del 12, 918 sidor stark, och icke mindre än 849 arter, varav många ytterligt närstående. Släktet *Allium* omfattar 228 arter och *Gagea* 72. Släktet *Heleocharis* har 38 arter, varav ej mindre än 24 i floran nybeskrivna. Av dessa stå 8 mycket nära *Scirpus uniglumis* och flera andra mycket nära *Scirpus palustris*.

Den linneanska arten *Empetrum nigrum* har uppdelats i icke mindre än 7 arter. Skillnaderna skola enligt nyckeln bestå i olika färg på de mogna bären (körsbärsfärgade eller svarta), enkönade eller tvåkönade blommor, ståndarsträngarnas relativa längd i förhållande till kronbladen, bladens form (lineära, elliptiska, förlängt elliptiska eller smalt äggrunda) och hårighet (glatta eller delvis håriga). Kombinationer av dessa karaktärer giva de 7 arterna. För Skandinavien uppgivas endast *E. nigrum* och *E. hermaphroditum* men i eurasiatiska arktis finnes ytterligare *E. sibiricum* i Ostasien, *E. androgynum* likaledes i Ostasien, *E. arcticum* i östra Nordsibirien och *E. Kardakovii* i Kamtchatka. Hade Amerika medtagits i bearbetningen hade säkert artantalet ytterligare ökats.

Det är närmast ägnat att förvåna, att i de hittills utkomna delarna av floran inte mer än 780 nya arter beskrivits (nykombinationer ej medräknade). Skulle recensenten vid sin behandling av floran i Alaska ha använt ett sådant artbegrepp hade det blivit nödvändigt att beskriva flera hundratal nya arter därifrån, då det är en allmän regel att arternas variationsbredd i Beringssundsområdet och särskilt i Alaska är mycket större än exempelvis i Skandinavien. Detta bottnar i att här tertiära eller åtminstone äldre kvartära populationer kvarstå relativt obeskurna, då klimatväxlingarna varit mindre betydande, medan endast den splittra av en sådan population, som kunnat både motstå istidens kyla och interglacialernas värme, blivit kvar i under istiden mera glacierade delar av den arktiska och tempererade zonen.

Olika systematiska grupper i floran ha bearbetats av olika personer och det är därför givet, att bearbetningarna äro mycket ojämna. Uppfattningen av arternas omfattning har varit rätt olika hos olika författare och deras intresse för att mera exakt ange utbredningen likaså. Grundlighet och vederhäftighet varierar även. I ett arbete av denna omfattning är ju detta ofrånkomligt. De olika författarnas högst olika botaniska skolning gör sig ibland gällande på ett iögonfallande sätt.

Medarbetarnas antal ha i de hittills utkomna delarna varit icke mindre än 54 nämligen:

E. Bobrov, A. Borissova, A. Bulavkina, N. Busch, E. Czerniakovska, B. A. Fedtschenko, A. Fomin, N. Gontscharov, S. Gorschkova, G. Grigorjev, A. Grossheim, V. Grubov, M. M. Iljin, N. Ivanovna, A. Jarmolenko, S. V. Juzepczuk, O. Knorring, V. L. Komarov, H. Krascheninnikow, V. Kreczetovicz, L. Kuprianova, O. Kuzeneva, I. Larin, E. Lavrenko, I. Linkzevski A. Losina-Losinskaja, V. Maleev, O. Muravjeva, N. Nazarov, V. Nekrassova, S. Nevski, P. Ovczinnikov, I. Palibin, N. Pavlov, E. Pobedimova, A. Pojarkova, M. Popov, J. Prokhanov, S. Roshevitz, N. Schipczinsky, B. Schischkin, L. Sergievskaja, K. Shaparenki, E. Sinskaja, V. B. Soczava, D. Sosnovski, E. Steinberg, S. Tamamschajan, A. Tolmatchev, J. Vassilczenko, V. Vassiljev, E. Wulff, A. Vvedevsky, G. Zinserling.

Denna lista ger en uppfattning av det stora intresse och stora arbete som nedlagts på denna flora.

Flera av medarbetarna ha avlidit under florans utgivningstid. På grund av de sparsamma underrättelserna kan ej alla dessa angivas, men Busch, Fedschenko, Fomin, Grossheim, Komarow och Nazarov äro nu döda.

Det är givet att ett arbete av denna karaktär och omfattning icke kan vara utan felaktiga eller uteglömda uppgifter.

Mycket få från området kända arter torde ha helt uteglömts. Man söker dock förgäves efter exempelvis *Oxytropis Sverdrupii* beskriven från Taimyrområdet av Lynge i »Maud»expeditionens vetenskapliga resultat 1918—25 No 1 sid. 8. Synonym som bort vara med saknas då och då exempelvis *Cherleria dicranoides* Cham. & Schlecht. på vilken *Stellaria dicranoides* (Cham. & Schlecht.) Fenzl är grundad. Uppgifterna om originallokal har tydligen berett författarna svårigheter, ibland på grund av språket, i andra fall kanske på grund av att originalbeskrivningen ej varit tillgänglig. Så uppgives t. ex. *Carex Buxbaumii* Wahlenb. vara beskriven från omgivningen av Leningrad, medan i originalbeskrivningen anges Östhammar och Lappland. Recensentens art *Rumex sibiricus* uppges vara beskriven från Kamtchatka och typen skulle finnas i Leningrad, men i originalbeskrivningen anges klart att typen är från Jenisej-mynningen och att den finnes i Stockholm. En och annan felaktig uppgift kan man finna i beskrivningarna, t. ex. då *Habenaria Chorisiana* som begåvats med namnet *Pseudodiphyllum Chorisianum* säges ha nästan rund läpp. Läppen är rektangulär.

I utbredningsuppgifterna insmyger sig oftare fel och ofullständigheter. Amerika är rätt ofta uteglömt när arealen angives, exempelvis på *Ranunculus sulphureus*. På *Dryopteris Linneana* har Kamtchatka glömts bort, på *Ranunculus Escholtzii* likaså och på *Ranunculus illyricus* och *sardous* Skandinavien. Tryckfel äro så vitt recensenten kan bedöma rätt sällsynta. Då *Scolochloa festucacea* uppges ha 10 cm breda blad skall detta givetvis vara 10 mm. *Eriophorum vaginatum* uppges vara beskriven i Species plantarum sid. 521 vilket skall vara sid. 52 osv. De flesta äro dock ej av störande art. Uppenbarligen har även den icke-ryska texten i citaten ingående granskats av någon person van vid europeisk text.

Utbredningsuppgifterna har särskilt intresserat recensenten. Området har uppdelats i 7 huvuddelar, Arktis, Europeiska delen, Kaukasus, Västsibirien, Ostsibirien, Fjärran Östern och Centralasien. Var och en av dessa delas vidare i 4—14 underavdelningar, så att sammanlagda antalet områden blir 49. (En översättning av dessa områdens beteckningar till engelska jämte kartor över dem och över de viktigaste bergskedjorna i Centralasien: »Geographical and other abbreviations in the Flora URSS by Komarov and others» har publicerats av Stearn i New Phytologist 46 No 1, 1947. Intresserade, som utan att kunna läsa de ryska bokstäverna önska begagna floran, hänvisas till denna uppsats). Varje växts utbredning angives genom uppräkning av de av dessa 49 områden, där den förekommer. Vore icke områdena av så ojämn storlek och ibland av olämplig form skulle detta ge en rätt god föreställning om utbredningen, men det största området, Lena—Kolyma, är lika stort eller större än hela Europeiska huvuddelen, vilken delas i 14 mindre områden.

Även områdena Obsk och Jenisejsk, som omfatta de stora skogsområdena vid floderna Ob och Jenisej, äro jättestora, flera gånger Skandinaviens storlek, medan å andra sidan de Centralasiatiska områdena äro valda mycket små, ett par äro endast av ett svenskt landskaps storlek. Det är givetvis växtgeografiska skäl som föranlett denna stor olikhet i områdenas

begränsning. Uppgifterna från det arktiska området bli ytterst summariska, då arktiska Sibirien tagits som ett enda område sträckande sig från Ural till Chukchhalvön. Sådana långa och smala områden äro otjänliga att använda vid utbredningsuppgifter. Det råder ingen tvekan om att respektive författare i många fall insett dessa olägenheter. Medan i de tidigare delarna utbredningsuppgifterna hålla sig strikt till de förutbestämda distrikten, ha i de senare ofta lämnats mera detaljerade uppgifter inom parentes. Härigenom har arbetet avsevärt ökat i värde som växtgeografisk källskrift.

Mestadels på grund av det använda snäva artbegreppet, men även av andra skäl, har i Flora SSSR uppgivits en hel rad arter för Skandinavien eller Fennoskandia, som vi icke bruka räkna med i våra floror. Då språksvårigheter torde göra att få, om ens någon, svensk botanist plöjt igenom detta digra verk för att få en uppfattning om dessa, kanske det kan vara på sin plats att räkna upp de arter, som recensenten av olika skäl vid en hastig genomgång funnit anmärkningsvärda ur skandinavisk synpunkt. I vad mån de böra föranleda ändringar i listan över vår flora bör bli föremål för bedömning i samband med uppgörande av en ny flora-lista över Skandinavien eller vid utarbetandet av en ny skandinavisk flora. Här nedan uppräknas dessa arter.

Equisetum litorale Kühlew. (= *E. arvense* var. *inundatum*) uppgives för Skandinavien.
Lycopodium appressum (Desv.) V. Petr. (= *L. Selago* f. *appressum*) uppgives för Skand.
— *pungens* La Pyl. (= *L. annotinum* var. *pungens*) uppgives för Skand.
Dryopteris rigida (Hoffm.) Und. (= *Aspidium rigidum* Sw.) uppgives för södra Skand.
Groenlandia densa (L.) Fourr. (= *Potamogeton densum*).
Stipa Joannis Čel. uppgives för Skand.
— *stenophylla* Czern. uppgives för Skand.
Calamagrostis elata Blytt. (= *C. purpurea* hos skandinaviska författare).
Agrostis maritima Lam. (= *A. alba* var. *maritima*) uppgives för Murmansk.
Poa turfosa Litw. (närstående *P. pratensis*) uppgives för Karelska Lappland.
— *pinegensis* Roshev. (= *P. sudetica* f. *pinegensis* = *P. pratensis* var. *pinegensis*) uppgives för Dvina-Petchora områder, men ej från Skand.
— *Ganeshini* Roshev. (närstående *P. glauca*) uppgives för Kola (Hibinä).
Heleocharis eu-uniglumis Zins. (= skandinaviska *Scirpus uniglumis* delvis).
— *fennica* Palla. (*Scirpus uniglumis* delvis) uppgives för Finska viken och Östersjöns stränder.
— *intersita* Zins. (= *Scirpus* »*mamillata* × *eu-palustris*») uppges för Karelska Lappland.
— *ovata* (Roth) Roem. & Schult. uppges för södra Skand.
— *septentrionalis* Zins. (*Scirpus uniglumis* delvis) uppges för Kola och Solovetzskiöarna.
Carex approximata Bell. (*C. membranacea* Hoppe) uppges för Kola och Karelen.
— *chlorostachys* Stev. (= *C. capillaris* f. *major*) uppges för Skand.

Carex discolor Nyl. (= *C. salina* ssp. *cuspidata* var. *borealis*) uppges för N. Skand.
— *emasculata* V. Krecz. (= *C. Buxbaumii* var. *heterostachya*) uppgives för Skand.
— *Grahamii* Boott. (= *C. vesicaria* var. *alpigena*) uppges för Kola (Hibinä).
— *hylaea* V. Krecz. (= *C. canescens* var. *subtenella*) uppges för södra Karelska Lappland.
— *inumbrata* V. Krecz. (= *C. caespitosa* var. *retorta*) uppges för Fenno-skandia.
— *marina* Dew. (= *C. glareosa* f. *elegantissima*) uppges för Kola, Svjatoj Nos.
— *omskiana* Meinsh. (närstående *C. elata*) uppges för Karelska Lappland.
— *paralia* V. Krecz. (= *C. maritima* Muell.) uppges för Kola.
— *retorta* (Fries) V. Krecz. (= *C. caespitosa* var. *retorta* Fries) uppges för Skand.
— *Siegertiana* Uechtr. (= *C. orthostachys* Trev. delvis).
— *stenolepis* Less. (= *C. rostrata* var. *borealis*) uppges för Kola.
— *stygia* Fr. (närstående *C. rariflora*) uppges för Karelska Lappland.
— *tripartita* All. (= *C. Lachenalii*).
— *wiluica* Meinsh. (närstående *C. Goodenowii*) uppges för arktiska Europa (har rapporterats från Kola av Zinserling).
— *vitilis* Fr. (= *C. brunnescens* var. *sphaerostachya*) uppges från Skand.
Juncus atrofuscus Rupr. (= *J. Gerardi* var. *atrofuscus*) uppges från Vita Havet.
— *Juzepczuckii* V. Krecz & Gontsch. (närstående *J. bufonius*) uppges för Nordeuropa.
— *ambiguus* Guss. (närstående *J. ranarius*) uppges för Finland.
— *nastantus* V. Krecz & Gontsch. (närstående *J. ranarius*) uppges för hela Europa.
— *inundatus* Drej. (= *J. balticus* var. *inundatus*) uppges för Finska Viken.
Orchis Fuchsii Druce uppges för Skand.
Polygonum linicola Sutulov (= *P. lapathifolium* f. *linicola* Schw.) uppges för södra Karelska Lappland.
Atriplex nudicaulis Boguslav. (= *A. praecox* Hylph.).
Echinopsilon hirsutum (L.) Moq. (= *Kochia hirsuta*).
Stellaria diffusa Willd. (= *S. Friesiana* = *S. longifolia* hos skandinaviska författare).
Silene uniflora Roth (= *S. maritima* With.).
— *polaris* Kleop. (närstående *S. Otitis*) uppges för Mezen och Archangelsk.
— *parviflora* (Ehrh.) Pers. (närstående *S. Otitis*) uppges för Leningrad.
— *paucifolia* Ledeb. (= *S. tenuis* var. *paucifolia*) uppges för arktiska Europa.
Coronaria Flos-cuculi (L.) A. Br. (= *Lychnis Flos-cuculi*).
Ceratophyllum Komarovii Kuzen. uppges för en parkdamm i Leningrad.
Anemone altaica Fisch. uppges för arktiska Europa.
Hepatica nobilis Gars. (= *Anemone Hepatica*).
Batrachium dichotomum Schmalh. (= *Ranunculus peltatus* var. *septentrionalis*).

Batrachium Kauffmannii (Clerc) V. Krecz. uppges för Skand.
— *Giliberti* V. Krecz. uppges för Ladoga-Iljmen området.
— *foeniculaceum* (Gilib.) V. Krecz. (= *R. circinatus*).
Ranunculus borealis Trautv. (= *R. acer* subsp. *Frieseanus*) uppges för Karelska Lappland.
— *megacarpus* W. Koch (= *R. americomus* var. *fallax*) uppges för Karelska Lappland.
Corydalis Halleri Willd. (= *C. solida*).
Rhodiola quadrifida (Pall.) Fisch. & Mey. (närstående *Sedum Rosea*) uppges för arktiska Europa.
Grossularia reclinata (L.) Mill. (= *Ribes Uva-crispa*).
Filipendula denudata (Presl.) Fritsch (= *F. Ulmaria* f. *denudata*) uppges för Skand.
Potentilla lapponica (Nyl.) Juz. (= *P. multifida* var. *lapponica*). Endem i Skand. — Kola.
— *Heidenreichii* Zimm. (närstående *P. intermedia*) uppges för Karelska Lappland.
Anthyllis Vulneraria L. har uppdelats i en rad arter:
— *arenaria* (Rupr.) Juz. uppges för Finland.
— *coccinea* (L.) Rech. uppges för Öland och Gotland.
— *colorata* Juz. uppges för Balticum.
— *Linnaei* Sag. uppges för Skand.
— *maritima* Schweigg. uppges för Balticum.
— *polyphylloides* Juz. uppges för Balticum.
Hedysarum arcticum B. Fedtsch. (= *H. obscurum* på Kola).
Medicago lupulina var. *Wildenowii* Bonn. uppges för Ladoga-Iljmen området.
— *borealis* Grossh. uppges från Ladoga-Iljmen området och från »Norra Europa?»
Frangula alnus Mill. (= *Rhamnus Frangula*).

Det är icke recensentens avsikt att här kritiskt undersöka dessa uppgifter utan endast att fästa uppmärksamheten på dem.

Flora SSSR. är tillgänglig på ett flertal svenska bibliotek. Tyvärr är detta ej fallet med ett par andra arbeten av intresse för vår flora. Jag syftar på Perfiljev, Flora Severnovo Kraja [Nordområdets Flora] och Goworuchin, W. S., Flora media boreali et polaris Uralensis, Sverdlovsk 1937. Exemplar av dessa arbeten synes icke vara möjliga att erhålla utanför Ryssland och alla försök att skaffa dem ha hittills strandat.

Riksmuseum den $^{8}/_{2}$ 1951. *Eric Hultén.*

A. H. Smith, Mushrooms in their Natural Habitats. 2 vol. — Portland, Ore., (Sawyer's Inc.) 1950. — Pris 26: 50 U. S. $.

Svampböcker med färgbilder produceras f. n. i stort antal i nästan alla länder. Det stora flertalet är naturligtvis av rent populär karaktär. Strängt vetenskapliga arbeten med deras höga pris och begränsade avsättnings-

möjligheter måste tyvärr bli mycket sparsamma. Rätt ofta publiceras emellertid arbeten, som ha något att ge åt såväl den vanlige matsvampsplockaren som den mera vetenskapligt sinnade mykologen.

I svampböcker av alla dessa kategorier är bildmaterialet av högst växlande beskaffenhet och kvalitet, både vad originalbilderna och reproduktionssättet beträffa. Akvareller äro väl alltjämt de vanligaste originalbilderna, och färgfotograferingen har hittills i ganska obetydlig utsträckning tagits i mykologiens tjänst. Det arbete, vars namn läses ovan, är, såvitt rec. har sig bekant, något helt nytt på svampböckernas område, om man nu får använda ordet bok om detta verk. Det består av två volymer, varav den första innehåller texten och är en verklig bok. Den andra volymen är däremot en nästan decimetertjock bokatrapp. När man öppnar denna, visar den sig innehålla ett »View-Master» stereoskop samt en instickspersm med 33 cirkelrunda skivor, var och en med infällda färgfoton av 7 svampar i form av Kodachrome filmer i format 11 × 12 mm. Sammanlagt illustreras sålunda 231 arter. Stereoskopet är försett med en enkel frammatningsanordning, varigenom man på ett ögonblick skiftar mellan de olika bilderna på samma skiva; utbytet av skivor är också blott ett ögonblicks verk. Stereoskopet ger en kraftig förstoring och bildskärpan är oklanderlig. De stereoskopiska bilderna äro utomordentligt goda. Färgerna växla givetvis med ljuskällan. Förf. rekommenderar, att stereoskopet riktas mot ett vitt papper kraftigt belyst av en vit matt glödlampa. Med tanke på att bilderna väl mest bli studerade, då det är mörkt ute, är det alldeles på sin plats, att färgåtergivningen skall vara korrektast vid artificiell belysning. Men tyvärr äro färgerna ej alltid så vällyckade ens vid föreskriven belysning. Var och en som något handskats med färgfoton vet, att färgfotograferingen ännu ej är alldeles pålitlig och att ytterst få bilder äro fullkomligt korrekta. Rec. gjorde själv mycket obehagliga erfarenheter härav under sitt arbete med kryptogamdelen av »Vilda växter i Norden». Där hade man dock möjligheten att vid reproduktionen i trefärgstryck söka rätta till färgerna. Med igenkännandets sorg finner rec. i dessa stereoskopbilder några av de vanligaste felen, såsom en violettgrå ton över hela eller nästan hela bilden eller en lysande rödbrun barrförna eller smaragdgröna skogsmossor och gräs. Rec. är visserligen ej någon skivlingskännare, och de exklusivt amerikanska svamparna äro honom totalt obekanta, därför kan han ej med sakkunskap yttra sig om alla svamparnas färger. Det är dock tydligt, att de i många fall ej äro fullt korrekta. Med någon vana att bedöma färgfoton kan man dock av omgivningen med rätt stor sannolikhet sluta sig till hur svampens färger böra korrigeras. Alla bilder synas dock vara fullt igenkännliga, och åtskilliga äro ypperliga. Mina anmärkningar drabba enbart färgfotograferingen i dess nuvarande utveckling, ej förf. eller producent, vilka var för sig gjort bästa möjliga arbete. Både den vetenskapliga mykologen, matsvampsplockaren och naturvännen böra med stor glädje och stor behållning kunna studera dessa bilder.

Arturvalet kan naturligtvis alltid diskuteras. De första 13 bilderna visa discomyceter (skålsvampar och murklor), de följande tre *Cordyceps*-arter. Härefter följa gelésvampar, fingersvampar, kantareller och tickor,

sammanlagt 14 bilder, 7 rörsoppar, 4 taggsvampar och ett dussin gastromyceter. De återstående äro skivlingar jämte allra sist några supplement till de tidigare grupperna. Bland skivlingarna äro exempelvis flugsvamparna företrädda med 15 arter, champignonerna med 9, riskorna med 13, under det att kremlorna räkna blott 5 representanter och spindelskivlingarna likaledes 5. Släkten av småskivlingar, sådana som *Mycena, Omphalia* och *Galera,* äro naturligtvis ganska sparsamt företrädda. Åtskilliga arter äro exklusivt amerikanska, men flertalet äro för en skandinav gamla bekanta. Några arter äro stora rariteter, t. o. m. några nybeskrivningar förekomma. Flertalet äro emellertid ganska allmänna, åtminstone i vissa delar av Nordamerika. En del allmänna arter saknas, och urvalet kan delvis synas rätt godtyckligt. Men även här vet rec. genom egen erfarenhet, att det i fråga om köttiga svampar är en sak att göra en önskelista för fotografering och en helt annan att få användbara foton av de önskade arterna.

Textbandet är en ansenlig volym (626 sid. i stor oktav). Några kapitel behandla bl. a. storsvamparnas förekomstsätt, deras ätliga och giftiga egenskaper, hur de skola insamlas och prepareras för herbariet. Ett innehållsrikt kapitel (45 sid.) ger den bästa och fullständigaste redogörelse rec. känner över skivlingarnas mikroskopiska karaktärer och tekniken för dessas studium. Huvudparten av volymen intages av beskrivningar på behandlade släkten och arter. Dessa beskrivningar innehålla avsnitt om arternas ätlighet och om förväxlingsmöjligheterna med andra arter men äro i övrigt rent vetenskapliga och fästa största avseende vid de mikroskopiska karaktärerna. Alla beskrivningar äro gjorda med förf:s vanliga utförlighet, åskådlighet och klarhet. Han har lagt vikt vid att alltid konservera de fotograferade exemplaren och att beskriva de mikroskopiska karaktärerna från just dessa exemplar. Examinationsschemata finnas till alla de avbildade arterna, men deras nytta kan starkt ifrågasättas. Ett schema till 5 godtyckligt utvalda kremlor eller till lika många spindelskivlingar fyller knappast någon förnuftig uppgift. Man undrar kanske också något, vilken läsekrets arbetet egentligen avser att vända sig till. För matsvampsplockaren och naturvännen torde det mesta av texten vara alltför svårsmält, och de för dem intressanta avsnitten äro ej särskilt lätta att hitta. Den vetenskapliga mykologen finner måhända en del av dessa avsnitt vara en onödig ballast och skulle säkerligen gärna sett, att förf:s egna åsikter om släktbegränsningar o. dyl. fått ett något större utrymme än de korta antydningar, vartill de nu inskränka sig. Den som vill börja ett mera vetenskapligt studium av skivlingarna torde aldrig kunna finna en lärorikare eller intressantare introduktion. För varje naturvän äro bilderna en upplevelse, och var och en som skaffat arbetet kommer säkerligen att flitigt använda stereoskopet. Det är därför att hoppas, att arbetet trots sitt pris skall få många köpare och beundrare även på denna sidan Atlanten.

J. A. Nannfeldt.

Mansfeld, Rudolf, Die Technik der wissenschaftlichen Pflanzenbenennung. Einführung in die Internationalen Regeln der botanischen Nomenklatur. — Akademie-Verlag Berlin 1949. 116 s., 8 pl.

Efter en kort inledning, som förklarar några nomenklatoriska grundbegrepp, lämnar förf. en likaledes kortfattad, men mycket innehållsrik framställning av den botaniska nomenklaturens historia från äldsta tider till de moderna nomenklaturreglernas tid. Man får här veta, att nomenklatursvårigheter icke äro något nytt; redan Columella (samtidig med Nero) klagade över vindruvsorternas förvirrade nomenklatur. Ytterligare några klassiska och medeltida författare och deras arbeten omnämnas; något utförligare behandlas Caspar Bauhin's »Pinax theatri botanici», den förlinnéanska tidens Nomenclator botanicus. Förf. citerar så Tournefort's sats av år 1694 »nomina breviora sint» och övergår till en redogörelse för Linné's verksamhet i den mån den berör nomenklaturen, varvid givetvis »Critica botanica» och »Species plantarum» ställas i förgrunden.

Innan förf. går vidare, redogör han för några från binär nomenklatur principiellt helt skilda principer för botanisk namngivning. Bland de omnämnda systemen är det i synnerhet två, som tilldraga sig uppmärksamheten, även om man vid första påseendet ej gärna vill taga dem på allvar.

Bergeret försökte 1818 att av på förhand definierade stavelser sammansätta namn så, att de blevo beskrivningar på den växt, de avsågo. De så uppkomna namnen bildades alltså i princip ungefär som den organiska kemiens namn, med vilka de också jämföras av Mansfeld beträffande längden. I detta system heter *Antirrhinum* (utan tillagt artnamn) *Gymnosporoplectroprosopanthus*. Förf. anmärker, att man kanske kunde tolerera längden och svårhanterligheten hos dessa namn, om de höllo, vad de lovade. Det göra de emellertid ej — till skillnad från den organiska kemiens namn. Härtill kunde ju anmärkas, att kemisterna funnit det nödvändigt — eller åtminstone lämpligt — att i fråga om ofta nämnda kemiska föreningar ersätta de långa namnen med kortare, som ej säga något om sammansättningen.

Om Bergeret's namn kunna jämföras med namnen på kemiska föreningar, kunna de av N. M. Wolf föreslagna namnen jämföras med de kemiska formlerna. Wolf försökte i två arbeten (1781 och 1786) ett system för namngivning, där varje stavelse motsvarar en viss del av växten, och där varje bokstav anger någon egenskap. I detta system blir exempelvis namnet på *Allium Scorodoprasum* Aô Wŷwo Pynarvae. — Intetdera av de nämnda systemen har kommit till nämnvärd användning.

Åt nomenklaturens utveckling från Linné fram till 1867 ägnar Mansfeld en kortfattad historik. Här hade man kanske önskat en utförligare redogörelse för »Kew-regeln», vilken nu kommit på en alltför undanskymd plats i förhållande till den roll, den spelat, bl. a. som norm för nomenklaturen i åtminstone de tidigaste delarna av de stora i Kew författade flororna över exotiska länder. Svenska botanister torde ha kommit i kontakt med denna regel mest genom 1907 års upplaga av Lunds Botaniska Förenings »Förteckning över Skandinaviens Växter», där den delvis tillämpats (t. ex. *Alnus rotundifolia*).

Som den första upplagan av de moderna nomenklaturreglerna torde Alphonse de Candolle's förslag »Lois de nomenclature botanique» av år 1867 kunna anses. Det antogs som normerande för botanisk nomenklatur på den av Société botanique de France nämnda år i Paris anordnade botaniska kongressen. De s. k. Wiener-reglerna, »Internationale Regeln der Botanischen Nomenklatur», antagna på den internationella botanistkongressen i Wien år 1905 och året därpå utgivna på franska, engelska och tyska, ansluta sig i allt väsentligt till »Lois». För huvudprinciperna och för de ändringar, som beslutades på de internationella kongresserna i Brüssel (1910), Cambridge (1930) och Amsterdam (1935) lämnar Mansfeld kortfattade redogörelser, likaså för »The American Code», »The Type Basis Code» och O. Kuntze's »Codex brevis maturus».

Största delen av Mansfeld's arbete ägnas åt en redogörelse för de gällande nomenklaturreglerna och deras sätt att verka. Författaren citerar de viktigaste paragraferna och förser dem med exempel och kommentarer. I stridsfrågorna intar han oftast en neutral refererande ståndpunkt, i ett och annat fall ställer han sig avgjort på den ena sidan och motiverar sitt ställningstagande, ibland rätt utförligt. I synnerhet gäller detta frågan, huruvida ett namns betydelse bör ha någon inverkan på dess användbarhet och giltighet. Han företräder den ståndpunkten, att ingen hänsyn får tagas till namnets riktighet ur språklig, geografisk eller morfologisk synpunkt, och ger onekligen tungt vägande skäl för sin åsikt, vilken vid första påseendet nog förefaller egendomlig. Beträffande tautonymerna (alltså namn av typen *Linaria linaria*) anser han, att strängt taget ingen giltig anledning finnes att förkasta dem, men att det dock är lämpligt att göra så med hänsyn till, att de alltid varit förbjudna i de av europeiska botanister tillämpade reglerna. Han påpekar, att exempelvis namnen *Arctostaphylos uva-ursi* och *Carum Carvi*, vilkas giltighet aldrig bestritts, äro tautonymer lika väl som *Linaria linaria*, fastän tautologien är camouflerad i det förra fallet av användandet av två skilda språk, i det senare av upprepning i annan kasus. I fråga om namn av typen *Sagina saginoides* anför förf., att de rent av kunna vara till nytta, då de ju antyda, att arten i fråga tidigare förts till ett annat släkte. Dessutom torde det vara svårt att formulera en regel, som utesluter alla tänkbara varianter av denna typ. Som exempel anföres, att det inte skulle tjäna något till att införa en regel, som förbjuder namnen *Luzula luzuloides* och *L. luzulina* men tillåter *L. luzulifolia*. Kasserandet av ur morfologisk synpunkt oriktiga namn skulle medföra stora praktiska svårigheter. Sådana namn förekomma i mycket större mängd, än man a priori vore böjd att antaga. Mansfeld är en av samtidens främsta orchidéspecialister, och från detta specialområde har han med förkärlek hämtat sina exempel, varför de kanske förefalla svenska läsare främmande och en smula likgiltiga. Ett av dem berör dock ett välkänt släkte: *Platanthera*, vars namn (= bred ståndarknapp) passar bra på *P. chlorantha*, men ej alls på *P. bifolia*.

En konsekvens av principen, att namnens betydelse ej får spela någon roll, blir, att rena skriv- och tryckfel ej skulle få rättas, vilket dock hittills varit tillåtet att göra. Enligt referentens mening måste åtminstone författaren själv ha rätt att ändra ett tryckfel, vilken rättighet borde kunna

utsträckas till misstag av annan art, om rättelsen göres, innan namnet i sin ursprungliga form hunnit bli allmänt använt. (Jfr KER-GAWLER's ändring år 1809 till *Lilium davuricum* av det år 1805 givna namnet *L. pennsylvanicum* för en i Östasien hemmahörande art). För en annan person än författaren kan det ibland vara svårt att avgöra, vad som är ett oavsiktligt tryck- (resp. skriv-) fel. Se t. ex. den advokatyr, som presteras beträffande namnet *Ledenbergia* i 2. upplagan av Engler-Prantl »Die natürl. Pflanzenfam.» Bd. 16 c s. 149, och MACBRIDE's kritik av denna i »Flora of Perú» II s. 553.

Föreskriften, att beskrivningen av varje ny systematisk enhet måste vara avfattad på latin, försvaras av MANSFELD med god argumentering.

Åt typ-metoden ägnas stor uppmärksamhet. Man noterar här med tillfredsställelse författarens påpekande, att de exemplar, som nu finnas i LINNÉ's herbarium i London, ej utan vidare få anses som originalexemplar till de i »Species plantarum» år 1753 namngivna arterna. Detta påpekande tycks ej kunna göras tillräckligt ofta.

I slutkapitlen behandlar författaren helt kortfattat tyska växtnamn och ger sina egna synpunkter på nomenklaturreglerna och deras tillämpning. Beträffande den vidare utvecklingen av reglerna är det författarens mening, att ytterligare ändringar av dem ej kunna tolereras; däremot böra de luckor, som alltjämt finnas, så snart som möjligt utfyllas. På tal om sådana nödvändiga kompletteringar anser förf. som ett oavvisligt krav »weitere Störungen der Nomenklatur durch das Ausgraben ganz alter, bisher allgemein übersehener Literatur in der Zukunft auszuschliessen». Häri måste man oreserverat instämma.

MANSFELD's bok vänder sig kanske i främsta rummet till dem, som ej behöva tränga särskilt djupt in i nomenklaturreglernas paragrafdjungel. De finna här ett svar på den ofta framställda frågan, varför det finns så många olika namn på samma art, och varför namnfrågor ofta äro så invecklade. Men även den, som måste studera reglernas grundtext i detalj, finner här många beaktansvärda synpunkter. Boken bör ej saknas på någon botanists bokhylla.

Erik Asplund.

FREAR, DONALD E. H., A Catalogue of Insecticides and Fungicides Vol. II. Chemical Fungicides and Plant Insecticides. — Waltham, Mass. U. S. A. 1948 (Ann. Cryptog. et Phytopathol., Vol. VIII).

Liksom första delen inledes även den andra med en redogörelse för det kodsystem, som användes vid katalogiseringen. Detta innebär, att varje grupp (eller annan konstituerande egenskap), som ingår i en kemisk förening tillordnas ett visst, här tabellerat tal, varigenom föreningen som helhet karakteriseras av en stigande följd sådana tal. Ordnandet eller sökandet av kemiska föreningar blir således lätt, när kodbeteckningarna införts, även om det artificiella draget i förfarandet blir påtagligt.

Listan över kemiska fungicider är ordnad efter detta system men upptar även det kemiska namnet (enligt Chemical Abstracts) jämte formel. En förkortning för substansens verkningsgrad och den art denna avser, an-

ges även, när detta är känt. En siffra hänvisar till litteraturförteckningen; åtföljes den av ett P är det på sedvanligt sätt fråga om ett patent, vars nationalitet litteraturförteckningen ger ytterligare besked om.

Den andra huvudlistan, »Plant Insecticides», är ordnad efter »Standardized Plant Names» (second edition, 1942) och anger i stort sett samma data som den nyss nämnda listan över kemiska fungicider och hänvisar till den gemensamma litteraturförteckningen.

Volymen avslutas utom av den tidigare nämnda litteraturförteckningen av en numeriskt ordnad förteckning över förekommande patent och ett index över de kemiska föreningarna. Denna sista förteckning, som är ordnad efter det välkända systemet i Chemical Abstracts, omfattar samtliga i såväl Vol. I som Vol. II förekommande, kemiska föreningar.

Arbetet, som med några reservationer gjorts så komplett som möjligt fram till januari 1944, kommer säkert att mottagas med tacksamhet av alla som syssla med hithörande problem. Det bör förkorta och underlätta litteraturstudierna avsevärt.

Olle Mårtensson.

E. M. Wakefield and R. W. G. Dennis, Common British Fungi. — Bungay, Suffolk (P. R. Gawthorn, Ltd) 1950, 290 sid., 111 färgpl., 6 textfig. Pris 35 sh.

Det har varit ett länge närt behov i England att erhålla ett modernt arbete, efter vilket det vore möjligt att bestämma makromyceter utan alltför stora svårigheter. Någon kritisk, brittisk svampflora av senare datum existerar ej och tidigare för ändamålet brukbara verk äro utgångna, svåra eller omöjliga att erhålla samt för dyrbara för gemene man eller för studerande, som önska tillägna sig mykologisk kunskap. På sådana grunder — och sålunda ej som ett tillskott till en redan alltför berikad litteratur på området — ha förff. med ett tacksamt arbetsfält och en mångårig, vetenskaplig erfarenhet givit arbetet en hög målsättning beträffande standard och exakthet.

»Common British Fungi» upptager illustrationer i färg av icke mindre än 470 »allmänna» arter jämte sådana som till följd av påfallande karaktärer eller av annan orsak ansetts böra vara med i sammanhanget. Att detta liksom arbetets för övrigt lättöverskådliga disposition i hög grad bidrager till dess instruktiva syftemål ligger i öppen dag. Efter en introduktion följer några upplysande och välskrivna kapitel om avhandlade svampars — skivlingar till *Boleter, Aphyllophorales* och *Gasteromyceter* — struktur och utveckling, klassifikation, insamling, examination och preparation. Under rubriken klassifikation inrymmes examineringsscheman fram till resp. släkten; därpå några ord om namnfrågor och litteraturanvisning med annotationer. Större delen av arbetet upptager dock, som sig bör, beskrivningar av släkten och främst av arter interfolierade med 111 färgplanscher (ovan anförda 470 arter). I betraktande av det betydande bildmaterialet, som till största delen är av förff:s egen hand, må sägas, att detsamma väl fyller sin uppgift att vara adekvat. Att en eller annan art antagit färgnyanser av främmande slag kan väl knappast

helt undvikas vid reproduktion av en sådan mångfald. Till arbetets många och stora förtjänster skall vidare anföras, att för arterna också medtagits avbildningar av sporer, cystider o. s. v. liksom att mått å desamma angivits vid beskrivningarna, de senare tillräckligt utförliga och korrekta, aldrig enformigt tröttande och ej sällan supplikerade av korta men värdefulla diskussioner och kompletterande upplysningar om arter, som ej medtagits. Kommer därtill träffande ståndortsuppgifter, upplysningar om arternas frekvens, förklaringar av latinska namn m. m. Att »Common British Fungi» givits ett sådant omfång, som här skett — det behandlar omkring en femtedel av Brittiska öarnas beräkningsvis 2 500 basidiomyceter — förtager knappast dess användbarhet även för den enbart mykofagiskt intresserade (tack vare just dess rika illustrationer och lätthanterlighet) samtidigt som arbetet utan gensago är en utomordentligt värdefull och efterlängtad hjälp för ett mera avancerat publikum. I slutet påträffas förutom index en förteckning över avbildade arter med angivande av lokal, ståndort och tidpunkt för insamling av avbildade exemplar, något som kan annoteras med tillfredsställelse. Tyvärr saknar man just sådana uppgifter alltför ofta i de fall, då man väl behöver dem. Boken, som har fördelen att vara förhållandevis billig, bör finna en god avsättning också i skandinavisk marknad. I densamma saknas ej heller nya rön och erfarenheter, varför den även av denna anledningen varmt kan rekommenderas den, som vill utöka eller uppfriska sin erfarenhet i allmänna drag och icke bara om »common British fungi».

Gustaf E. Haglund.

Lousley, J. E., Wild Flowers of Chalk & Limestone. — The New Naturalist. Collins, London 1950. 48 pl. i färg, 24 pl. i vanl. tryck, 16 kartor, 254 pp. Pris 21 s.

»The New Naturalist» - serien, ur vilken tidigare Turrill's »British Plant Life» anmälts i denna tidskrift, har som sitt mål att »interest the general reader in the wild life of Britain by recapturing the enquiring spirit of the old naturalists». De hittills i denna serie utkomna arbetena, av vilka även Blunt's »The Art of Botanical Illustration» och Pearsall's »Mountains and Moorlands» böra nämnas, ha samtliga bidragit att fylla detta mål på ett utomordentligt sätt.

Näst efter »British Plant Life» är Mr. Lousley's bok om kärlväxterna på krita och kalksten enligt anmälarens mening den bästa i serien. Det första kapitlet behandlar i korthet några allmänna frågor, såsom huvuddragen av kalkbergarternas utbredning i Britannien, deras roll som substrat för kärlväxterna, hur kalkens utbredning i detalj kan avläsas genom vissa arters förekomst etc. I två följande kapitel skildras Box Hill i Surrey, ett av London-bornas mest omtyckta utflyktsmål, numera delvis naturskyddat och ägt av The National Trust. The Council for the Promotion of Field Studies har här helt nyligen anlagt en biologisk station. Områdets flora beskrives i det första av dessa avsnitt. Man finner på Box Hill, det utförligast behandlade av krit-områdena, flertalet av de viktigare kalkväxter vilka sedan återkomma på andra håll. Det andra av de kapitel,

som ägnats Box Hill, skildrar väsentligen det ekologiska sambandet mellan kritan och dess växtvärld men ger också — ytterst knapphändiga — upplysningar om växtsamhällena med tonvikten lagd på deras succession. De senare är schematiskt indelade i »Chalk grassland», »Chalk scrub» och »Chalk woodland» (en betydligt fylligare framställning av den engelska kritans intressanta associationer återfinns t. ex. hos TANSLEY, British Islands and their Vegetation, och i uppsatser av SALISBURY och TANSLEY i Journal of Ecology). Härefter följer i magistralt skildrade kapitel — förf. tycks känna varje fotsbredd av brittiska kalkmarker — de olika områdena av kalk och krita med deras flora från Kent i öster till Aran Islands i väster, från Isle of Wight i söder till Firth of Forth i norr. Varje avsnitt är rikt illustrerat med planscher och kartskizzer.

Det synes självfallet, att ett arbete som behandlar floran på ett geologiskt begränsat och definierat substrat också bör ägna avsevärt utrymme åt utbredningen och differentieringen av detta. Det är emellertid på denna punkt som en allvarlig invändning kan resas mot LOUSLEY's framställning. Ty de korta notiserna i första kapitlet och de på en trycksida sammanförda och i alltför liten skala reproducerade kartorna över de ifrågavarande bergarternas utbredning är under inga omständigheter tillräckliga för att tillfredsställa läsarens aptit efter geologiska fakta. Som bekant är Britanniens geologiska uppbyggnad en ganska komplicerad historia; här finns flertalet geologiska perioders kalkstensbildningar mosaikartat representerade från de prekambriska, starkt lokala bäddarna i Skottland och Wales till de kenozoiska kalkstenarna på Isle of Wight. Förf. urskuldar sig med att han själv inte är geolog. Man tycker kanske att bristerna borde varit lätta att avhjälpa; enbart ur den korta och starkt koncentrerade framställningen av Britanniens geologi i den 5. upplagan av LAKE & RASTALL's lilla Textbook of Geology (London 1941) skulle åtskilliga allmänna upplysningar kunnat hämtas vilka kunde ha varit av stort intresse för LOUSLEY's första kapitel.

Förf. anser att i England 5 kärlväxter är av speciellt värde som kalkindikatorer, inte minst därför att de är vanliga och har en vidsträckt utbredning. De är *Buxus sempervirens*, *Clematis vitalba*, *Helianthemum nummularium*, *Sorbus aria* och *Viola hirta*. Såsom absolut kalkskyende framhäver förf. främst *Calluna* och *Erica cinerea*.

Den brittiska floran på krita och kalk är oerhört rik. Där finns givetvis först och främst en hel rad av våra vanligare mer eller mindre kalkbundna arter, sådana som *Anthyllis*, *Arabis hirsuta*, *Calamintha acinos*, *Cirsium acaule*, *Clinopodium*, *Linum catharticum*, *Phleum phleoides*, *Primula farinosa*, *Saxifraga tridactylites*, *Seseli libanotis* och *Sesleria coerulea*. Även *Hyoscyamus* betraktas som kalkbunden, förf. har i allmänhet observerat den på jordhögar utanför vildkaninernas hål. Arten är ju näringsfordrande och trivs icke i sluten vegetation. Men också de stora sällsynteterna från våra mest extrema kalkområden påträffas här, så t. ex. är *Anacamptis*, *Cephalanthera damasonium*, *Orchis mascula* och *Orchis ustulata* närmast karaktärsväxter för den engelska kritan, medan *Aster linosyris*, *Helianthemum canum*, *Orchis militaris*, *Senecio integrifolius* och andra är mer lokala till sin utbredning. På kalkmarkerna uppe i Skottland finns ett

antal av våra nordiska basibiontiska fjällväxter, *Arenaria norvegica, Bartsia alpina, Dryas octopetala, Saxifraga hypnoides* och några till. Men för den som sysslat med nordisk kärlväxtvegetation är det kanske ändå en annan grupp arter som erbjuder den största tjusningen, nämligen sådana som förekommer på kalkmarkerna i Britannien men som saknas i de svenska. Med hänsyn till de påfallande likheterna mellan Nordeuropas och de brittiska öarnas flora är det märkligt att icke mindre än ett 90-tal säkert spontana brittiska basibionter saknas i Sverige. Hit höra exempelvis *Ajuga chamaepitys, Asperula cynanchica, Atropa belladonna* (en vanlig karaktärsväxt för kritan), *Blackstonia perfoliata, Daphne laureola, Helianthemum polifolium, Hippocrepis comosa, Linum anglicum, Polygala austriaca* och *P. calcarea, Rubia peregrina, Sedum dasyphyllum* och *Trinia glauca*. Flertalet hithörande är främst lokaliserade till Sydenglands krita; de är i allmänhet mellaneuropeiska resp. sydeuropeiska arter som här har sina nordvästligaste utposter. Representanter för den starka östliga steppkomponenten i Ölands, Gotlands och Estlands alvarfloror saknas i stor utsträckning. Däremot finns många motsvarigheter till den sydeuropeiska klippsnårskomponent, som hos oss t. ex. representeras av *Coronilla emerus*. Ett antal andra utbredningsgrupper äro även företrädda. Så är den rent mediterrana *Arbutus unedo* på Västirland mest lokaliserad till kalkförekomster. Arten utgör ju som bekant ett av de märkligaste inslagen i den irländska floran. En liten grupp av speciellt växtgeografiskt intresse bildar vidare de i Wales endemiska *Sorbus*-arterna (*S. bristoliensis, S. leyanus, S. porrigens* och *S. vagensis*), en motsvarighet till den rika *Sorbus*-floran på Norges västkust.

Lousley's bok om floran på brittisk kalk och krita är ett i den populära genren ganska sällsynt arbete. Genom den levande men sakliga stilen som aldrig blir torr eller ansträngd trots att texten är späckad med fakta, genom de utomordentligt reproducerade färgfotografierna och genom den gedigna sakkunskap och den kärlek till ämnet som lyser igenom på praktiskt taget varje rad, har boken blivit ovanlig och stimulerande. Man kunde önska att större hänsyn tagits till regionala geologiska fakta, liksom att någon plats ägnats växtgeografiska sammanfattningar. Men intet är fullkomligt och kritik är ju alltid lätt att åstadkomma. »The New Naturalist», författare, förlag och redaktion, är att gratulera till en ny fullträff!

Henning Horn af Rantzien.

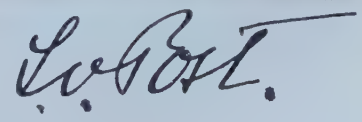
LENNART VON POST

$^{16}/_{6}$ 1884—$^{11}/_{1}$ 1951.

AV

OLOF H. SELLING.

Foto 1929.



En hövdingagestalt, ett av den svenska vetenskapens stora namn, gick den 11 januari med Lennart von Post ur tiden. I åtskilliga år hade han dragits med ohälsa och i det längsta sökt rädda åt sig den arbetstid han kunde få; han visste att hans dagar var räknade. Ett av de viktigaste av hans arbeten väntade på fullbordan, men helt nådde han inte fram: det var verket som i 20 år förberetts om Viskadalens senkvartära nivåförändringar. Långt tidigare hade han i en följd av arbeten, ett av den art som bildar epok i internationell forskning, säkrat sig en ledarställning inte bara på sitt egentliga fält, geologien. I botaniken var hans namn mer känt och erkänt över världen än de flesta svenska botanisters, och det var naturligt att han till kongressen i Amsterdam (1935) blev en av vicepresidenterna i sektionen för geobotanik, ekologi och växtgeografi. Hans produktion var till stor del geobotanisk, han blev efter Rutger Sernander torvmarksforskningens ledare i vårt land, och framför allt var han den, som gjorde pollenanalysen till en forskningsmetod av yppersta rang. Det är den botaniska delen av hans gärning, som här skall tecknas mot bakgrunden av hans liv och personlighet som forskare och människa.

Ernst Jakob Lennart von Post var västmanländning och föddes den 16 juni 1884 på Johannisberg i Lundby socken utanför Västerås. Fadern, auditören Carl Fabian von Post, var under olika perioder även advokat,

vice häradshövding, mönstringskommissarie och lantbrukare. Det blev denne, som fick hand om hans uppfostran. Modern, Beata Nisbeth, avled redan följande år, och några syskon hade han inte. I viss mån satte det sin prägel på hans personlighet. På fädernet härstammade han närmast från militärer och auditörer av ättens första rangelska gren; hans farfars far, majoren Olof Jakob Rangel, 1809 adopterad von Post, hade luktat krut vid Anjala. Innan släktkedjan bakåt förtonar i västgötabyn Rangedal i Rångedala — nära Viskadalen, där Lennart von Post utförde sin levnads sista stora verk — skymtar på 1600-talet den lärde prästen Petrus Rangelius. På mödernet åter bråddes han på skotska och baltiska krigare med inslag från den i paleobotaniken inte obekanta ätten Sternberg, och morfadern var hovman.

Av allt detta ärvde Lennart von Post intresset för den svenska jorden, klarheten och logiken, läggningen för det lärda, det bålda och mönsterherrens blick. Den ecklesiastiska ådran rann däremot sparsamt, och typen för en hovman var han inte alltid. I juni 1901, ännu inte 17 år fyllda, blev han student i Västerås med högsta betyget i — förutom kristendomskunskap — historia och naturalhistoria; han skulle också en gång komma att medverka i Historisk Tidskrift. På hösten gjorde han entré i Uppsala, imposant redan då och med naturstudiet i blickfånget, väl medveten om sin duglighet. Det rådde ingen tvekan om att detta var ett forskarembryo, som smakat vetenskapens svärdspets. Han högg först in på zoologien, men inte långt efteråt kom han till A. G. Högboms fascinerande föreläsningar, och det gick med honom som med flera andra: han blev geologisk konvertit. Med hans historiska läggning kan omvändelsen knappast varit svår. Snart nog var han även etablerad i Rutger Sernanders krets. Kontakten med Sernander släppte han aldrig. Den inspirerade stora delar av hans gärning, och för att förstå vad den betytt, behöver man inte ha tagit del av hyllningen till 75-årsdagen (D. N. 31/10 41: »Rutger Sernanders rikspark») eller av minnesorden i Ymer 1944. I Uppsala träffade han också sin frände Hampus von Post, den åttioårige forskarpionjären, som då ännu levde med i förhandlingarna. Okänt är emellertid om Hampus hälsade också Lennart von Posts första forskningar med de vresiga knarranden från sina stövlar han gärna åstadkom, när någon lät torvmossarna vittna om klimatväxlingar.

I början av 1902 stod Mästarmyrs utdikning för dörren. I Botaniska Sektionen höll Sernander den 5 mars ett föredrag om de gotländska myrarna, och efter det hade Lennart von Post sin första vetenskapliga uppgift. Han skulle nu, medan tid var, utreda Mästarmyrs utveckling. I sällskap med Jakob Ljungqvist, som tog hand om växtsamhällena, reste han ut med fullt pådrag. Den magnifika gotlandsskildringen »Kalkens och solens ö» (1940) liksom t. ex. föredraget i radio om »Markens naturmonument» (1935) ger oss ännu något av stämningen under dessa veckor. Ända från början trivdes han bland breda gotlandsbönder. »Bondeliv levde de», skriver han, »bondekläder buro de, ett bondespråk talade de, som det i början ville till att förstå. Men herremän voro de till hjärta och själ.» Det storvulna och överdådet hos dem gav genklang. Och när ölstopet gick runt, var von Post inte den, som tackade nej.

Det dröjde ett kvartsekel innan undersökningen av Mästarmyr låg i tryck, i beskrivningen till kartbladet Hemse. Men till våren 1903 var von Post färdig med sitt första tryckta vetenskapsalster, en beskrivning av litorinavallen vid Snoder i Sproge, som med sina inlagrade supramarina avsnitt gav anledning till jämförelse med Järavallen i Limhamn. Arbetets botaniska trumfess var fyndet av en fossil maskrosfrukt; man trodde den var den första kända, och upptäckten firades i Sernanders sällskap med en lagom fuktig supé. Lennart von Post var som student glad bland de glada, och hans intresse för växter och djur svalnade inte om de var anrättade. »Väcker du mig också mitt i natten, skall jag åtaga mig att äta en festmiddag», är ett av hans bevingade ord från den tiden. Han skaffade sig cykel för att banta men av motionen blev aptiten bara värre. Hans rörlighet trots allt väckte respekt. Maklig var han inte, det var hans vilja och forskarhåg för starka till, och han deltog med liv och lust i Högboms, Wimans och Sernanders exkursioner; ofta var han även ute ensam. »Grandiflorus» blev hans namn, när han senare tog inträde i S. H. T. i Uppsala. Det ger hans kynne och typ. Halva 1903 och hela 1904 var han amanuens på Geologicum. Efter tre års studier var han också klar med en fil. kand.: laudatur i geologi (Högbom), cum ins i zoologi (Tullberg); och geografi (Ahlenius), kemi (Cleve) och matematik (Falk) som fyllnad. En av hans elever, geokemist, präglade över 30 år senare i en skämtsam stund den lilla elakheten om von Posts »stora men obesvarade kärlek till matematiken»; det statistiska sinne, han obestridligen hade, var empiriskt. Fil. lic. blev han 2 ½ år senare, i december 1907, och i examen hade han både geologi och ett approbatur i jämförande fornkunskap. Han hade sällat sig till Knut Stjernas seminarium och berättade därifrån gärna om den majmorgon 1905, då han vid grävningar på platsen för nuvarande »Köttbasilikan», saluhallen vid S:t Eriks torg, var med om att finna en sotig, punschdoftande lagbok med dateringen »gammal utåv helvite». Stjerna var länge upprörd den dagen, men von Post gladdes.

Han var nu väl armerad med akademisk rekvisita, helst som han 1905 -06 hos Juel gjort också de botaniska övningskurserna för högre betyg i fil. kand.-examen. Någon disputation blev det aldrig för hans vidkommande. Det kunde ju också göra detsamma. Han var rustad för sitt verk. Tjugo år senare, i maj 1927, kallade Stockholms Högskola honom till filosofie hedersdoktor, och senare fick han äregraden från både Königsberg och Köpenhamn.

Licentiatavhandlingen gällde norrländska torvmossar i vad Högbom 1902 kallat »lidernas region». Arbetet hade börjat 1904 med Frans Kempe som mecenat och bakom det låg, fast det inte sägs, Högboms önskan att få en utredning för sitt stora verk »Norrland» (1906). Det schema von Post upprättade över myrarnas utveckling fann han på äldre dagar vara riktigare än det borde vara med de förutsättningar, som då fanns. Metodiken var vid den tiden ännu outvecklad och någon full bild av förloppen kunde inte ges. Svårigheten var främst att nå en tillnärmelsevis exakt tidsbestämning. I södra och mellersta Sverige fanns konnexioner med fornfynd och strandlinjer att tillgå, men här uppe fick

han extrapolera, därtill i en annan naturgeografisk miljö. Helt visst blev också resultatet osäkert, och han ansåg det själv vara tvivelaktigt om han hittat rätt mer än i enstaka fall. 24 år senare, när »Norrländska torvmossestudier» — som i titeln åtföljts av en optimistisk etta — till hans egen oförställda stolthet fick sin andra del, kunde han med pollenanalysens hjälp dra upp så mycket klarare huvudlinjer i skogens och myrarnas postarktiska historia i södra Norrland. Till denna senare undersökning hade Gunnar Boobergs arbete på Gisselåsmyren givit anledning.

Med sitt första torvmossearbete vann von Post 1906, vid 21 års ålder, sin första vetenskapliga utmärkelse, Vetenskapssocietetens Linnépris. Han återvände i oktober som amanuens till Geologicum, och där blev han kvar ännu ett år.

Redan till sin första undersökning hade han haft understöd från Sveriges Geologiska Undersökning. 1905 tillhörde han undersökningens torvmarkskommission, som arbetade i Närke. Kontakterna blev med tiden flera. Fr. o. m. 1908 blev von Post knuten dit, de första tre åren som vikarierande amanuens och geolog, sedan som tjänsteman (efter löneregleringen 1914 = statsgeolog). I undersökningens tjänst utförde han under 21 år sina främsta arbeten av dem, som hittills nått offentligheten; under denna tid fick den pollenanalytiska metoden den form den skulle segra i, och torvinventeringen kom till. Med pollenanalysen följde grundläggande skogshistoriska arbeten, med torvinventeringen förbättrade metoder för torvmarkernas studium och undersökningar av deras byggnad, uppträdande och genetiska system.

Han blev undersökningens torvexpert, och när han kom dit var han redan engagerad i förberedelserna för geologkongressens torvmarksexkursioner 1910. De resulterade i de viktiga skrifterna om Närkes fornsjöar och torvmossar. På denna från Sernanders undersökningar klassiska mark tillämpade von Post senare resultat och synpunkter och med sin blick, sin uppslagsrikedom och metodiska energi gjorde han nya, viktiga framsteg. Hans teknik var ändamålsenlig men blev aldrig subtil. Medarbetare från Vilstaängen 1908 ha i gott minne hur han hippopotamiskt tog sig ut i gölarna och borrade medan han trampade vatten. På land hade han verktygen bundna i tåtar runt om sig och när han reste sig, verkade det tältförankring. Det var nu han gav en ny floristisk indelning av Närkes vegetationshistoria och på den limnotelmatiska kontaktens utbildning urskilde olika igenväxningstyper bland fornsjöarna; här påvisades också den hastiga senglaciala (= finiglaciala) klimatförbättringen som en motsvarighet till Sernanders subatlantiska klimatförsämring. Han gjorde även växtsociologi på Skagershultmossen (1907). Resultatet av den undersökningen kom i en kongressguide 1910, där von Post och Sernander författat var sin del. Den förtjänar betecknas som en milstolpe i vår kännedom om mossars vegetation; bl. a. innehåller den de första kartorna över svensk mossevegetation och de första detaljerade över mossevegetation över huvud taget (Du Rietz). Sedan pålbyggnaden i Alvastra upptäckts 1908, utsträcktes (1909) von Posts utvecklingshistoriska arbeten till Dagsmosse vid Tåkerns sydvästra del, och även om den framträdde han 1910 med några meddelanden. Den spelade senare en viktig roll

i hans skrift om källmyrarna (1916). En växtgeografisk karta över Tåkern tillkom under hans ledning 1909 men utgavs inte förrän tjugo år senare.

Under kongressen, där von Post också var kommissarie för polarutställningen, deltog han inte direkt i den stora generalmönstringen av senkvartär vegetations- och klimatforskning. För Sveriges vidkommande sköttes representationen av Gunnar Andersson och Sernander. Det blev en duell, som skarpt visade motsättningarna mellan de båda falangerna, som von Post 1916 kallade den paleofloristiska (Andersson) och den paleofysiognomiska (Sernander). Det sköts rejält på båda håll, och von Post höll Sernander med ammunition; han var på rätt sida. Det var den sista stora sammandrabbningen i en tjuguårig strid. Vid 10-talets mitt uppgingo de båda riktningarna i den moderna vegetationshistoriska forskning, som fick pollenanalysens tecken och von Post till anförare.

Pollenanalysens tillkomst har även på senaste tid varit föremål för skiftande tolkningar. Den är von Posts centrala insats, och det kan därför vara befogat att följa den i detalj, fast det blir en utvikning.

Den växte gradvis fram. Fossilt pollen uppmärksammades först av H. R. Göppert i Hessens miocen i februari 1836 och en avhandling i ämnet, »De floribus in statu fossili commentatio», utkom samma år. 1837 fann Ehrenberg *Pinus*-pollen i Nordsveriges kvartär. Göppert pläderade 1841 för en (visserligen endast kvalitativ) inventering av avlagringars polleninnehåll. Ströuppgifter om kretaceiska till kvartära fynd finnas på åtskilliga ställen i 1800-talets litteratur. Utom Göppert och Ehrenberg bör schweizaren J. Früh räknas till pionjärerna. I sina »Kritische Beiträge zur Kenntnis des Torfes» (1885) behandlade han både sporer, träd- och örtpollen. Kvantitativa uppskattningar möta första gången — därtill med relativa tal — hos C. A. Weber 1893 (Bot. Jahrb. Beibl. 40 o. 43), och andra följde 1896. Sarauw gjorde 1897 räkningar i Danmark, men utan procenttal.

Pollenanalysens grundläggande principer förelågo alltså redan, då Gustaf Lagerheim mot slutet av 90-talet började hjälpa svenska och danska torvmosseforskare med pollenbestämningar. Lagerheim var detektiven, som gladdes åt identifieringen, och von Post hade Lagerheims hjälp redan till sitt första arbete. Ända till 1905 arbetade Lagerheim endast kvalitativt. Det året publicerade han i en uppsats av Witte (»Stratiotes aloides L. funnen i Sveriges postglaciala aflagringar», GFF 27: 7) en liten tabell, som i procentvärden visade de inbördes relationerna mellan *Alnus-*, *Betula-*, *Picea-* och *Pinus*-pollenet i tre skikt av Kvarnhalsmyren vid Länna utanför Uppsala. »Att häraf draga några slutsatser, är naturligtvis mycket vanskligt», skriver han. »Emellertid torde ju de stigande procenttalen af *Picea* särskilt böra papekas.» Det var ett viktigt drag han därmed kom på spåren, men iakttagelsen var inte ny. Redan tidigare hade Harald Lindberg publicerat liknande i Finland, och för Weber hade samma sak stått klar. von Post själv, som för pollenbestämningar haft Lagerheim till vägledare, bidrog till att ge dennes notis en smak av absolut pionjärskap; det gjorde han bl. a. i sina föreläsningar. Det är berättigat endast om man ser saken strängt lokalt. Ännu 1937 räknade han

med orätt Lagerheim som den kvantitativa pollenanalysens första namn. Han var det bara i den meningen att von Post idéhistoriskt, efter vad det verkar, inte tog arv av hans föregångare. Det fick för von Post räcka. På litteraturbehandlingen kunde han ibland ta ganska lätt. Weber kände han ju väl; de hade upprepade gånger exkurrerat tillsammans.

För sitt första norrländska arbete ansåg von Post, som han sade, det inte vara mödan värt att räkna pollen. Men när han 1908 arbetade på närkesmossarna, stod han inför den brännande frågan om stubblagren var samtidiga — som Sernander menade — eller inte. Han kom då att tänka på granpollenet och gjorde en uppskattning med hjälp av växtsociologiens Hult—Sernanderska skala, den femgradiga. »Pollenräkning ansåg jag då ännu inte behöva användas annat än i högtidliga fall», hette det i en föreläsning (26/4 37). Han fick ändå det uttryck han åsyftade. »Grangränsen» eller »granpollengränsen», som han 1909 kallade den, var användbar för lokala konnexioner.

Samma år återkom Lagerheim i N. O. Holsts »Postglaciala tidsbestämningar» (S. G. U., C: 216) med en utförlig analys av pollen från Kallsjö mosse i Skurup. För två skikt beräknade han procenttalen för tall, björk, al, alm (avtagande uppåt), ask, ek, lind (tilltagande) och hassel (räknad utanför som i senare pollenanalyser). Som Holst säger och Lagerheim för honom framhållit var här funnen »en säker *metod* att på mikroskopisk väg ... *lager efter lager noggrant följa såväl invandringen* af alla de växter, hvilkas pollen eller sporer uppträda fossilt, som också förändringarna i afseende på dessa växters relativa antal». Han hade anledning tacka Lagerheim för, som han skriver på separatet, det »kraftiga samarbetet». Tack vare det hade han kommit att formulera något så närstående modern pollenanalys, som möjligt var — utan att nå själva kärnan. Det skulle von Posts öga och metodiska energi till för att få fatt på den. I ett intressant arbete hade Steusloff 1905 varit inne på samma banor utan att i huvudfrågan komma längre.

Det är här det drar ihop sig. von Post fann att metoden med granpollengränsen, sådan han använt den 1909, var otillräcklig. När han 1913, i »Stratigraphische Zweigliederung», skulle visa att Webers hårt kritiserade »gränshorisont» verkligen fanns, tog han därför ett steg till och gjorde tabeller över kvoten *Picea* : *Pinus* i successiva lager. Då han så i Skåne skulle få fatt i liknande gräns som den granens uppsving markerade, en bokgräns, befanns det att bokpollengränsen inte var tillräcklig. Så började han räkna allt trädpollen. Han hade turen att i det avgörande skedet komma in på ett material från Bjärsjölagårds mosse i södra Skåne, som var gynnsamt. Det var 1915. »Då såg jag vad som kunde göras, och jag bearbetade även mitt material från Närke» föll hans ord i den nämnda föreläsningen. Bearbetningen bedrevs nu med all ihärdighet. Ganska snart prövade han idén att spåra skogseldars framfart i diagrammens björkuppslag. Ty von Posts stora bidrag, som kom pollenanalysen att slå igenom och bli ett första rangens arbetsinstrument, är diagramformen och påvisandet, genom systematisk genomarbetning av ett stort material, att de kurvor han fick fram, kunde konnekteras på sin rytm. Jag tror nog att Erdtman gjorde rätt, då han 1921 talade om »Die pollenanalytische Ar-

beitsmethode nach L. von Post», fastän han 1943 avsvor sig den formuleringen till Lagerheims fördel. Skall man nämna von Posts föregångare, bör man rätteligen tala om »metoden enligt Weber—Lagerheim—von Post». Man kan nog vara ense om att först med den form von Post gav den, blev pollenanalysen i princip färdig. Det är därför hans föredrag inför 16. Skandinaviska Naturforskarmötet i Kristiania 1916, »Skogsträdpollen i sydsvenska torvmosselagerföljder» är ett av naturforskningens klassiska bidrag.

Det var väl inte en tillfällighet att pollenanalysen fick sin form i Norden, i ett tidigare nedisat område och i ett slättland. Det har sagts om Linné att han kanske inte kommit sitt system så på spåren om han inte hamnat i ett en gång nedisat, någorlunda nykoloniserat land, där artbeståndet kan överblickas och gränserna i det är tämligen klara. Detsamma kan nog sägas om von Post och pollenanalysen. Där han arbetade fanns betingelserna: skogar av ett fåtal, klimatiskt gripbara arter med gynnsam pollenproduktion, därtill ett slättland, där dessa skogars skiftande sammansättning utan starkare störningar registrerades i fossila pollenspektra. I ett berglandskap hade det inte givit sig på samma sätt och inte heller i ett område med rik variation inom arterna och mer diffusa gränser mellan dem. Att man sedan kan tillämpa metoden även i de mest skilda miljöer är en annan sak, som för somliga varit svår att inse, ty läsarten får varieras. Pollendiagram är känsliga instrument — Hesselman talade en gång om »pollenlyror» — och sättet att spela på dem inkluderar överblick och sunt förnuft. Inte minst därför blev von Post mästaren. Han miste inte skogen ur sikte för trädens skull. Naturligtvis fick han i några fall uppleva att ingen är profet i sin egen stad. Det hade varit egendomligt annars.

De första diagrammen i tryck ingå i skriften om källmyrarna 1916. De följdes av en litteratur om f. n. grovt räknat 2 000 nummer, därav några handböcker. Bredvid Gerard De Geers lervarvsmätning har ingen metod så som den pollenanalytiska revolutionerat vår uppfattning om kvartär naturgeografi i vidaste bemärkelse, och sedan 1927 är den på god väg att göra detsamma för tertiären. Som stratigrafiskt hjälpmedel blev den naturligtvis oumbärlig och att dess verkningar sträckte sig till arkeologien var givet. von Post själv gjorde åtskilliga arkeologiska dateringar, främst den av Gerumsmanteln (1925). Han gav vid flera tillfällen stora översikter av vad pollenanalysen gick för i kvartära sammanhang, så 1924 och till skogsforskarkongressen 1929. Det gällde därvid skogshistorien i Europa, vars revertens och regionala parallellism han demonstrerade i eleganta diagramsynteser från Auvergne till Kilpisjärvi, från Luzern till Enare och till Ural. Hans förenklade treperiodsschema för Europas senkvartära klimat- och vegetationsutveckling (1929, 1930) kan med framgång tillämpas över hela Jorden. En triumf var det, när pollenanalysen 1937 genom Firbas fick forntidens åkerarealer inom sin räckvidd och icke minst när den året efter genom Fromms bearbetning av Lidéns material kunde anknytas till geokronologien. I april 1944, när von Post för pollenanalysen fick Vega-medaljen, tecknade han i breda drag det globala perspektivet, som han länge varit inne på. Då hade

metoden, som snabbt spred sig till Europa och något senare (1927) till Nordamerika, av honom själv — på material som Caldenius samlat — överförts till södra halvklotet (Sydamerika 1929, 1931, Nya Zeeland 1936), och genom hans förmedling hade den också börjat tillämpas i tropikerna. Denna sista stora sammanfattning, som av Godwin översattes till engelska, är på ett sätt hans pollenanalytiska bouppteckning och testamente.

Den andra stora insatsen under åren som statsgeolog var torvinventeringen. Den startade 1917, sedan världskriget kommit intresset för landets torvtillgångar som energikällor att sprida sig till riksdagen. von Post samarbetade med Gavelin för förslaget (1916) och kunde bygga på en försöksinventering han 1912—15 lett på S. G. U:s ordinarie anslag. På J. G. Anderssons initiativ togs linjetaxeringen, som använts på Värmlands skogar, till hjälp vid den förrådsstatistiska utredningen, som avsåg kännedom om torvmarkernas allmänna beskaffenhet. Jämsides med linjeinventeringen bedrevs den kvalitativa rekognosceringen, som avsåg detaljkunskap om torvmarker med en yta om minst 5 har inom 5 km från större kommunikationsleder.

Torvinventeringen var ett omfattande företag och när den var som störst arbetade 24 rekognoscörer i fältet. Närmaste män var Sandegren, Halden, Granlund, Willén, Gösta Lundqvist och som kemister Booberg och Assarsson. Staten var dubbelt så stor som för alla andra S. G. U:s undersökningar tillsammans. Det hela fick ett brått slut 1923, när den thorssonska besparingsaktionen satte in. Linjeinventeringens fältarbeten var visserligen slutförda och hade givit över 21 000 sidor protokoll, 56 000 rörprover och 6 000 prov för kemisk analys. Men den kvalitativa rekognosceringen, som skulle avslutats 1928, måste stoppas och utdragen ur kortregistret publicerades bara för 13 kartblad. Bearbetningen fick inknappade anslag — det gick 1927 så långt att högre instanser greps av vad Geijer kallat »negativ torvpsykos» — och von Post själv förlorade efter hand intresset. »Södra Sveriges torvtillgångar» kom bara i en första del (1926), men den var viktig nog. Den bidrog till att hålla svensk torvmarksforskning på internationell tätplats. Viktigt var inte minst det torvmarkernas genetiska system, som nu uppställdes, klart och tydligt, utan inblandningar av deskriptivt botaniska eller topografisk-morfologiska bisynpunkter. Det grundades på det till myren levererade vattnets karaktär: topogena, ombrogena och soligena myrar. När Osvalds »Myrar och myrodling» kom ut och bjöd på viss divergens, ägnade von Post på våren 1937 flera föreläsningar åt sitt system, som han ingående försvarade.

Andra viktiga resultat skall inte förglömmas: översiktskartan över Sveriges myrmarker (1927), Granlunds gradualavhandling (1932) och dennes kartor för dvärgbjörk, skvattram och klockljung i Syd- och Mellansverige (1925). von Post hade i instruktionen ryckt in bestämmelser att inte bara lagerföljd, fossil och myrsamhällen utan också en rad växtgeografiskt intressanta element skulle antecknas. Själv fick han viktiga tillägg till sin uppsats om *Cladium* och dess märkliga historia i Sveriges postarktikum (1925). Den hade varit planerad sedan över ett årtionde. Den blev, som mycket annat vad von Post gjorde, bara en preliminär studie, men naturligtvis elegant och givande. Torvinventeringens prov-

serier hade han också tänkt sig som ett pollenanalytiskt forskningsmaterial, som skulle spara honom tid. 1922 fick han också anslag för en genomarbetning. Så tillkom uppsatsen om de sydsvenska skogarnas regionala historia (1924), som innehöll bl. a. pollenanalytiska kartor för de postglaciala huvudskedena och en fördelning av diagrammen på fyra regionala typer, Skåne-, inlands-, västkust- och nordliga typen. En femte, bergslagstypen, kom i arbetet om Svea Älv (1928), som var ett omfattande försök att bevisa att Sveafallet vid Degerfors använts av Ancylussjön.

Ganska snart fann han emellertid att utvecklingen gick de gamla planerna förbi. Provtätheten i torvinventeringens material var för liten för att möta den nya tidens preciserade fordringar.

Med inventeringens resultat hade von Post ytterligare befäst sin ställning i torvmarksforskningen. Han kallades (1926) att ge riktlinjer i dess skånska tillämpning inför Fysiografiska Sällskapets torvmossekommission. Nu var också utmärkelsernas tid kommen. 1927 invaldes han av fysiograferna, kom också in i Lantbruksakademien, och samma år kom det första hedersdoktoratet.

Jämsides med allt detta hade han gjort ren geologi, både strandlinjer — en gammal kärlek från 10-talets början — och geotekniska undersökningar. 1914—22 hade han tillhört Statens Järnvägars geotekniska kommission. Agrogeologi hade han varit inne på, då han sommaren 1911 på J. G. Anderssons initiativ arbetade i Alnarp på de klassiska marker, där Nathorst 1870 funnit de första spåren av en glacialflora. Han hade också — i en bok, som aldrig nådde längre än till ett korrektur i hans bokhylla — skrivit en mästerlig översikt av den kvartärforskning han stod mitt uppe i. När »J. G.» gick till Östasiatiska Samlingarna efter att en kort tid ha gästspelat på Stockholms högskola, och professuren i allmän och historisk geologi skulle återbesättas, samlade von Post ihop sina meriter. I oktober 1927 höll han provföreläsningar men valde inget ämne, som kunde misstänkas för botanik, utan »Jordskred och orogenes». Han skulle snart ändå få känna på att han vågat syssla med en gränsvetenskap som gick in på botaniska domäner. Han fick tre av fyra förord till första rummet, men vid avdelningens röstning nej tack från alla utom en. Ännu i styrelsen anfördes mot honom att hans arbeten rörde sig »på gränsen till botanik» och hade underlättats av en statlig halvmiljon (torvinventeringen m. m.). Tio år senare hörde jag honom nämna detta med botaniken på ett sätt, som visade att minnet levde, och kanske påverkade det hans med åren minskade intresse för botanisk pollenanalys. Den 6 juni 1929 blev han emellertid utnämnd. Det hade gått med honom så som han — i några tryckta verser på daggstänkta bergens melodi och under pseudonymen P. V. Trannel — skaldat till De Geers 60-årsdag (1918):

Efter slika vilda bragder
blev den domen honom sagder:
»Till Högskolan drage Du i livstidsinternat!»

Nu hade högskolan givit honom De Geers professur, och förväntningarna var ömsesidiga. Själv satte han i början som vanligt till alla klutar. Han tog hand om elever, var de första åren som en bland dem och blev

på den tiden uppskattad. Exkursioner höllos till olika delar av landet, han samarbetade med växtbiologerna i Uppsala, han exkurrerade också med läroverkslärare och folkbildningskurser. Hans intresse att popularisera slog ut i blom på nya fält. De båda skogshistoriska skrifterna i Verdandis serie trycktes, och man kan beklaga att Sernanders önskan om översättning till världsspråk (D. N. 21/8 33) aldrig blev verklighet. Men von Post var nu en gång sådan, att han inte tänkte mycket på utländska relationer, ja, han hade t. o. m. svårt att sända brev och separat. En av de två höjdpunkterna i verksamheten på hans institut kom med den kurs, som »Kommittén för baltiskt kulturellt samarbete» under riksantikvariens ledning hösten 33 förlade dit. Den andra hörde till våren 38, då festskriften till De Geer förbereddes. Han startade 1932 den stora undersökningen av Viskans dalgång, utredningen av havsytans senkvartära nivåförändringar och landhöjningens gång i förening med en skogshistorisk konnexion via pollenanalysen. Baltiska Kursen gav upphov till Die Bålen-See-Studien (1935), som emellertid aldrig kom sig riktigt. Med Sten och Maj-Britt Florin, hans trogna medarbetare under största delen av professorstiden, gjorde institutet ändock en stor, central insats i sörmlandsforskningens tecken, och därifrån utgick nyheten om vindruvor i stenåldersböndernas diet. Elever anlände, utom från grannländerna, från Cambridge och Aberdeen och Reykjavik, ja, ända från Nya Zeeland, för att medarbeta i det pollenanalytiska stationsnätet. Själv reste han inte mycket; han klagade ibland att ekonomien band honom. I England hade han varit 1930 till kongressen i Cambridge, där han inledde det vegetationshistoriska symposiet. British Associations sammankomst i Norwich 1935 förde honom ånyo dit och till Skottland, och samma år for han till Holland. »På botanistkongress i Amsterdam» är en av de schvungfulla artiklar han skrev i Dagens Nyheter (14/9). Året därpå var han på kvartärkonferensen i Wien, träffade altmeistern Penck och exkurrerade i österrikiska Alperna.

Mina första intryck av von Post hör till denna tid. Han hade just kommit hem och skulle föreläsa. Hans botaniska gärning kunde ju ingen undgå att känna, och jag tänkte att där borde finnas kontakt; på det håll, där jag hölls, var intresset för gångna tiders växtvärld inte starkt. I sal 4 i den grå byggnaden vid Kungstensgatan väntade den 6 oktober en handfull studiosi med blicken på dörrhålet. Det verkade på något sätt björnbur. Tunga, litet stötiga, mjukt klapprande steg nalkades, och in kommer »Den Store», som han kallades, kastar i farten en välbevågen nick åt vänster och stoppar inte upp förrän framme vid fönstret. Efter en gir placerar han händerna i ansiktshöjd på pekpinnen och blicken i takkanten, dröjer litet, och sedan kommer i välformade perioder — ibland avbrutna av en sammanbiten emfas — en klar framställning av sekundärt avlagrat pollen som felkälla. Under en paus borrar han ögonen i novisen med ett forskande uttryck, en fortsättning av den koncentration han använt på förberedelserna. Innan föreläsningens början hade han väl, som han brukade, vandrat av och an i sitt rum med händerna innanför västen medan han planerade. Jag skulle senare många gånger se honom så.

C. Mannerfelt foto.

Lennart von Post i aktion.
Torvborrning i oktober 1937.

Förhoppningarna om kontakt sveks inte. Snart blev jag indragen i hans strålkrets. Även om han hade svårt att hålla kvar studerande, hade han en storartad förmåga att attrahera med vida vyer, och han levde med i vad han sade; kanske vädrade han en proselyt. Föreläsningarna övergick till Deckenschotter i Alperna, den nyvunna bekantskapen, och blev i speciellaste laget. Hans föreläsningar kunde vara glänsande men ibland också massivt prövande. Ingen föll precis i golvet, men det fanns tillbud bland de halvhjärtade. Nej, det var inne på institutet han kunde tala en varm om vegetationshistorisk forskning. När jag så fått pengar till en fornsjöundersökning, som han så när gjorde till en — förvisso trevlig — seminarieexkursion, och med pensel i handen plockade makrofossil ur torvproverna, var han en mäktig stimulans, som fortsatte så länge jag var kvar. Nästan varje dag slogs dörren upp, och in klev von Post för att få senaste framsteg. Det är givet att med regelbundna ronder tråden kunde tvinnas tunn, men han trivdes och det smittade. Själva julafton kunde han komma upp för att inleda med sitt litet stötiga: »Nåå, hur har det gått i dag.» Våren 38 var som nämnt en höjdpunkt, och motsvarighet till den kollektiva arbetslust, han då skapade, har jag inte sett. Redan tidigare hade emellertid bilden skuggats och en åtstramning i rekryteringen börjat märkas, han höll för höga fordringar och hans tentamina, efter frågelista och med tentator rakt framför offret på halvannan meters håll, var ingenting för svaga nerver. Högsta betyget höll han inlåst som en kronjuvel ända tills hans vän Hans W:son Ahlmann vid den tiden kom

honom på andra tankar, och tre elever formligen inbjöds att förvärva den. Visst kunde han vara hård och krigarsläktens påbrå märkas, och gärna berättades historien från Vingåkers hotell, där ett kvickhuvud, som sänts att svara på telefonen, återkom till bordet med ett »De e telefon till major von Post». »Majoren» genomskådade det hela, och när han kom tillbaka, låg det moln kring pannan. Trots allt som i vetenskapen uträttades och trots alla goda ansatser i begynnelsen, blev det få, som disputerade hos honom. Han koncentrerade sig mer och mer på sina egna arbeten, »Viskan» framför allt. När fältarbetena gick för fullt, så t. ex. sommaren 1940, hade han åtta medarbetare för lasset, och själv var han den aktive ledaren i sina gula shorts och uppknäppta skjorta, sina vita damasker och sin lilla vita skärmmössa, som gav intryck av tävlingscyklist. I samband med Viskan var det jag först såg honom författa, sent en vårnatt på institutet. Det låg tankarnas kondensation i luften och papper med hans kraftiga handstil på bordet, där han satt vid det öppna fönstret, i skjortärmarna, med en ritning framför sig. Den var full med svarta prickar, ännu inte särskilt upplysande, men han var entusiastisk och den blev ett relationsdiagram, som kan beses i hans hyllning till De Geer. Han arbetade alltid intensivt. Exkursioner kunde han så gå upp i, att han ensam stod en timme på Centralen innan spärren öppnades. På huvudet i en torvgrop eller med cigarretten i handen framför torvborrande elever var han i sitt esse. Men han kunde också koppla av, inte minst vid lunchen i biblioteket. »Profetkäket» var ett ställe, där nyheterna kom och gick.

Han var matematisk-naturvetenskapliga avdelningens promotor i maj 1939 och talade i Stadshuset klingande svenska till sakta musik, en vetenskaplig melodram. Nordstjärnan hängde nu på fracken. Han hade blivit 55 år och nått den ålder, då erkännandena börja komma villigare. Ledamot av Vetenskapsakademien hade han blivit samma år. Våren 1941 gav Göteborgs Högskola honom och Helge Backlund Sixten Heymans pris för författare och vetenskapsmän, och i juli blev han hedersdoktor i Königsberg. 1943 fick han ledamotskap av Vetenskapssocieteten i Uppsala, 1944 Vegamedaljen och till 60-årsdagen en festskrift, 1946 invaldes han i Danska Videnskabsselskabet, 1948 i Norska Vetenskapsakademien, och vid den tiden kom också Nordstjärnans kommendörstecken, andra klassen, och hedersledamotskap från Royal Irish Academy, Svenska Växtgeografiska Sällskapet och Dansk Geologisk Forening. Hedersdoktoratet i Köpenhamn 1950 är tidigare nämnt.

Redan då Heymanska priset kom, hade hans hälsa visat tecken att vackla. På tåget till Horred i augusti 1939, några dagar innan kriget bröt ut, fick han ett lätt slaganfall med tillfällig tungförlamning; han trodde det var »plåtmussle»-förgiftning. Men senare kom sjukdomen igen, och han förstod, att hälsans dagar var förbi. Hans produktion inskränkte sig huvudsakligen till yttranden efter föredrag och preliminära meddelanden om Viskan. Vegaföredraget »Pollenstatistiska perspektiv på Jordens klimathistoria» (1944) är den enda större uppsats av annat slag han publicerar. Han talar i det om allt som blivit ogjort. Viskan tar all hans tid. Artiklarna bli färre i Dagens Nyheter, där han sedan tio år ofta återkom-

mit med glansfulla exposéer i vitt skilda ämnen, från Cimbrernas åkrar (17/1 34), Pollenanalysen och forntidens jordbruk (6/10 37), Våra vattenväxters geografi (18/2 35) och Daggkåpor (8/5 43) till löss, glacialmorfologi, urberg och istidsteorier. Man träffar honom och frågar om ett nyutkommet arbete i pollenanalys, och han suckar med Kossinnas ord till Ambrosiani: »Ich lese keine Bücher.» Viskan är hela tiden i hans tankar. Vid Svenska Botaniska Föreningens årsmöte i november 1945 deltar han för sista gången i stockholmsbotanisternas offentliga förhandlingar; föreningens medlem hade han varit de första femton åren (1907—22). Strax efteråt utses han till sakkunnig för limnologiprofessuren i Lund men avsäger sig.

De sista åren blev en kapplöpning med tiden, och en skugga föll över hans tillvaro. Regelbundet halv åtta var han uppe vid busshållplatsen i Freskati för att fara till arbetet. Två onsdagkvällar i månaden kunde man se honom, stödd på käpp, tungt vandra uppför backen till akademiens sammanträden. Sjukdomsperioderna blev tätare. Mellan dem tog han i, ofta för hårt, och det förbättrade inte. Mot slutet av 1950 recenserar han Fægris och Iversens »Textbook of Modern Pollen Analysis», som han fått sig tillägnad. Han ser den som fältstecknet för en ny era, som tar vid, där hans slutar. Först skall han bara fullborda monografin över Viskadalens senkvartära fornfjord med dess bekräftelse på att han nått sitt mål med pollenanalysen. »Sedan», säger han, »avträder jag från den pollenstatistiska arenan.» Några veckor senare var han borta.

*

Lennart von Post var som en stor, kraftig ek, bred, tung i virket, vidfamnande, högre än de flesta i sin omgivning och fast rotad i svensk miljö. Skarpblicken fanns där ständigt, den framträder på många porträtt, och ingen som han talat med i ämnen som intresserade honom, kunde undgå att märka den. Den kunde ibland, som när pollenanalysen utarbetades, nå de höga höjderna, särskilt om det var fråga om grafisk framställning; där hade han sin särskilda styrka. Han var uppslagsrik och hade vida intressen, och frågor, som han fångades av, gick han upp i; det var, som nämnt, intensitet över hans göranden. Han hade järnvilja i den momentana kraftutlösningen. Halvhet, slentrian, brist på omdöme, oförmåga att fatta det han tänkte och ville gjorde honom otålig, för att inte säga ovänlig, och han kunde konsten att frusta gnistor. Otålighet var ett påtagligt drag. Den kan utläsas ur porträttet i festskriften till 60-årsdagen. Med all den magnifika styrkan och behärskningen på ytan fanns där något nervöst, något spänt i hans väsen. Han var höggradigt impulsiv, under klang- och jubelåren på 30-talet ibland påfrestande labil, men det mildrades med åren. Han kunde ha ett barns oberäknelighet, brusa upp, glömma och vilja försoning på kort stund. Ömhet har tillskrivits honom, men det är inte rätta ordet för den påtagliga välvilja och uppmuntran han kunde visa sina medarbetare. Snarare var det en välvilja, som, bunden av ett slags tafatthet i psykologiska detaljer — eller kanske ett mindre utpräglat sinne för dem — ivrigt sökte sin form. Att lösa knopar av

psykologisk art var inte hans linje. I det långa loppet var hans välvilja för elever heller inte av det, djupare sett, personliga slaget. För det var han alltför koncentrerad på sin egen uppgift, och det fanns väl en och annan, som i stillhet tyckte, att han ibland mest premierade raska dragare av imperatorsvagnen. Han kunde särskilt fascineras av människor, vilkas arbete han icke följt på nära håll; sådant är dock mänskligt. Han hade andra kvaliteter. Han var vänfast mot dem, som intresserade honom, han var rejäl och rättfram. Han hade humor av det massiva slaget, och när han skrattade, kom det hjärtligt och fullviktigt. Hans pondus var inte artificiell. Den framträdde både till vardags och fest. Det var klang och must, när han talade och skrev. Beundran och respekt och ett slags återhållen tillgivenhet väckte han även hos dem som aldrig kom honom nära eller som hade åsikter skilda från hans. Det är skada, att det inte finns fler av hans resning.

Förteckning över Lennart von Posts skrifter med helt eller till någon del geobotaniskt innehåll.

GFF = Geologiska Föreningens i Stockholm Förhandlingar.
SGU = Sveriges Geologiska Undersökning.

1903

En profil genom högsta Litorinavallen på södra Gotland. — GFF, 25: 5, s. 257—258. [Ref. av föredrag.]

En profil genom högsta Litorinavallen på södra Gotland. — GFF, 25: 6, s. 339—372, 4 fig., pl. 10—11.

1906

Norrländska torfmossestudier. I. Drag ur myrarnas utvecklingshistoria inom »lidernas region». — GFF, 28: 4, s. 201—308, 12 fig., pl. 10—12.

1909

Exkursionen i västra Närke och till Loka-dalen den 14—16 maj [1909] [tills. m. J. G. Andersson]. — GFF, 31: 5, s. 404—411, 4 fig.

Om Skarbysjö-komplexet och dess dräneringsområdes postglaciala utveckling. — GFF, 31: 5, s. 282—284.

Stratigraphische Studien über einige Torfmoore in Närke. — GFF, 31: 7, s. 629—706, 14 fig., pl. 23—24.

1910

Das Skagershultmoor. — Ingår i: L. von Post & R. Sernander, Pflanzenphysiognomische Studien auf Torfmooren in Närke. — XI. Intern. Geol. Congr., Guide 14 (Excursion A 7), s. 1—24, 14 fig., pl. 1—4. Stockholm.

Om Närkes fornsjöars hydrografi och postglacialtidens klimathistoria. — GFF, 32: 2, s. 232—237.

The Pile-Dwelling at Alvastra. b) Geological deductions. — Ingår i: H. Munthe, Studies in the Late-Quaternary History of Southern Sweden. GFF, 32: 5, s. 1274—1277, 1 fig.

1911

En exakt geologisk tideräkning. — Populär Naturvet. Revy, 1: 1, s. 11—20, 5 fig.

Ref. av N. O. Holst, Efterskörd från de senglaciala lagren vid Toppeladugård. — GFF, 33: 7, s. 533.

1912

Die Torfmoore Närkes. — C. R. XI. Sess. Congr. Géol. Intern. (Stockholm 1910), 2. Fasc., s. 1277—1287, 3 fig. Stockholm.

Några nya lokaler för fossil Trapa i Sverige. — GFF, 34: 2, s. 380—384.

Vulkaner och varma källor på Spetsbergen. Ett nytt moment i Spetsbergens geologi. — Populär Naturvet. Revy, 2: 2, s. 49—61, 12 fig. [paleoz.-rec. växter].

Yttrande med anledning av R. Sernanders föredrag om nordvästra Tysklands högmossar. — GFF, 34: 5, s. 472.

Rec. av J. P. Gustafsson, Bidrag till torfmossarnas geologi samlade från småländska torfmossar, I, II. — GFF, 34: 2, s. 273—276.

Rec. av H. Hesselman, Jordmånen i Sveriges skogar. — Populär Naturvet. Revy, 2: 4, s. 152—153.

Rec. av N. Hartz, Bidrag til Danmarks tertiære og diluviale Flora. — GFF, 34: 3, s. 368—370.

1913

Alnarpstraktens Geologi. — Ingår i: H. Winberg, Landtbruks- och Mejeriinstitutet vid Alnarp samt Alnarps egendom under tiden 1862—1912, s. 181—212, 8 fig., 1 karta. Göteborg.

Mosse. — Nordisk Familjebok, 2. uppl., 18, sp. 1196—1201, 1 fig. Stockholm.

Über stratigraphische Zweigliederung schwedischer Hochmoore. — SGU, Ser. C: 248 (= Årsbok 6: 2), 52 s., 11 fig.

1915

En bestämning af Ancylusgränsen i norra Västmanland. — GFF, 37: 4, s. 341—342, 1 fig.

Ett egendomligt jordskred i västra Värmland. — GFF, 37: 5, s. 567—582, 2 fig.

Ett fynd av fossil Trapa natans i västra Värmland. — GFF, 37: 4, s. 343.

Yttrande med anledning av Th. G. Halles föredrag om Jämtlands kalktuffer. — GFF, 37: 4, s. 281—282.

Yttrande med anledning av G. Samuelssons föredrag »Om den klimatiska innebörden af hasselgränsens och några andra gränslinjers tillbakagång inom Skandinavien». — GFF, 37: 3, s. 191—192.

1916

Einige südschwedischen Quellmoore. — Bull. Geol. Inst. Upsala, 15, s. 219—278, 14 fig., pl. X—XIII.

Om skogsträdpollen i sydsvenska torfmosselagerföljder. — GFF, 38: 6, s. 384—390. [Ref. av föredr.; se 1918.]

Sveriges geologiska undersöknings förslag till en förrådsstatistisk undersökning av torvmarkerna inom Götaland och Svealand utom Dalarna [tills. m. A. Gavelin]. — SGU, Ser. C: 274 (= Årsbok 9: 10), 50 s.

Yttranden med anledning av eget föredrag »Om skogsträdpollen i sydsvenska torfmosselagerföljder». — GFF, 38: 6, s. 392—394.

1918

Ett finiglacialt granfynd i södra Värmland. — GFF, 40: 1, s. 19—23.

Instruktion för förrättningsmännen vid Sveriges Geologiska Undersöknings förrådsstatistiska torvmarksundersökning. — 16 s.; Stockholm [anonym; omtr. i von Post & Granlund 1926, s. 25—37].

Skogsträdpollen i sydsvenska torvmosselagerföljder. — Forh. ved de skand. naturforskeres 16. møte, 1916, s. 432—465 [sep.: s. 433—465], 2 fig. Kristiania.

Sveriges lösa jordlager. — Ingår i: I. Flodström, Naturförhållandena i Sverige, s. 89—144, 25 fig. Uppsala.

Yttranden med anledning av eget föredrag om »Skogsträdpollen i sydsvenska torvmosselagerföljder». - Forh. ved de skand. naturforskeres 16 møte, 1916, s. 466—467 och 468. Kristiania.

1919

Ett par offerdammar från Skånes bronsålder. — Rig, 2: 2—4 (= Studier tillägnade Oscar Almgren), s. 160—176, 13 fig.

Yttranden med anledning av H. Hesselmans föredrag »Om pollenregn på hafvet och fjärrtransport af barrträdspollen». — GFF, 41: 2, s. 99—105, 107—108.

1920

Postarktiska klimattyper i södra Sverige. — GFF, 42: 5, s. 231—241.

Yttrande med anledning av B. Haldens föredrag om tvebottnade sjöar. — GFF, 42: 2, s. 55.

1921

»Allmänna upplysningar» och »Arbetets utförande». [Utdrag ur: »Instruktion för förrättningsmännen . . .» (se nedan).] — 3 s.; Stockholm [anonym].

Instruktion för förrättningsmännen vid Sveriges Geologiska Undersöknings kvalitativa torvmarksrekognoscering. — 19 s.; Stockholm [anonym].

Kartbladet n:r 52 Upperud [tills. m. N. Willén]. — Ingår i: Beskrivning till kartbladet Upperud. — SGU, Ser. D: 52, s. 1—34, 1 karta.

Stora Dode mosses geologi och fyndens geologiska ålder. — Fören. f. fornminnes- och hembygdsvård i sydöstra Skåne, Skr. I, s. 23—32.

Torvmarker. — Ingår i: H. Munthe, Beskrivning till kartbladet Burgsvik jämte Hoburgen och Ytterholmen. — SGU, Ser. Aa: 152, s. 104—113, 2 fig.

Torvslag och torvmarkstyper. — 1916 års torvkommittés betänkande, s. 1—14. Stockholm.

Upplysningar rörande Sveriges geologiska undersöknings torvmarksrekognoscering. — Ingår i: Beskrivning till kartbladet Upperud. — SGU, Ser. D: 52, s. I—XVI. [Se äv. 1922 o. 1923.]

1922

Pollenanalytisk undersökning av bisonkranier från Hagebyhöga och Mjölby. — Ingår i: H. Munthe, Ett par fynd av bison från Östergötland i ny belysning. — GFF, 44: 1—2, s. 148—149.

Sveriges Geologiska Undersöknings torvinventering och några av dess hittills vunna resultat. — Svenska Mosskulturfören. Tidskr., 1922: 1, s. 1—27, 3 fig.

Upplysningar rörande Sveriges geologiska undersöknings torvmarksrekognoscering [se 1921]. — Ingår som s. I—XVI i: Beskrivning till kartbladet Vänersborg (utdrag ur torvmarksregistret). — SGU, Ser. D: 42; och Kartbladen Uddevalla, Fjällbacka och Strömstad (utdrag ur torvmarksregistret). — SGU, Ser. D: 41, 51 o. 61 [1 vol.]. [Se äv. 1923.]

1923

Dagsmosse och Dr. Cleve-Eulers gungningshypotes. — GFF, 45: 3—4, s. 367—375, 1 fig.

Pollenanalytisk åldersbestämning av björnkäke från Snöstorp (Halland). — Ingår i: E. Lönnberg, En märklig subfossil björn från Halland. — Fauna och Flora, 1923: 4, s. 152—153.

Södra Sveriges torvtillgångar enligt Sveriges Geologiska Undersöknings torvinventering. — Nord. Jordbrugsforskn., 1923: 5—8 (Berättelse för Nord. Jordbrugsforsk. Foren. kongr., Göteborg 1923), s. 320—333, 1 fig.

Upplysningar rörande Sveriges geologiska undersöknings torvmarksrekognoscering [se 1921, 1922]. — Ingår som s. I—XVI i: Kartbladen Göteborg och Borås. — SGU, Ser. D: 32 o. 33; Kartbladet Ulricehamn (utdrag ur torvmarksregistret). — SGU, Ser. D: 34; Kartbladet Skara (utdrag ur torvmarksregistret). — SGU, Ser. D: 43; Kartbladen Hjo och Linköping (utdrag ur torvmarksregistret). — SGU, Ser. D: 44 o. 45; Kartbladen Mariestad och Karlsborg (utdrag ur torvmarksregistret). — SGU, Ser. D: 53 o. 54.

1924

Dagsmosse och Dr. Cleve-Eulers gungningshypotes. Slutord. — GFF, 46: 5, s. 534.

Das genetische System der organogenen Bildungen Schwedens. — Com. intern. Pédol., IV Comm. (Rom 1924), No. 22, s. 287—304.

Ett exempel på pollenanalytisk åldersbestämning. — GFF, 46: 5, s. 551—552.

Torfuntersuchungen bei S. G. U. — Com. intern. Pédol., Vème Comm. (Rom 1924), »État de l'étude et de la cartographie du sol, publ. Inst. Geol. al Romăniei», s. 245—246. Bukarest.

Ur de sydsvenska skogarnas regionala historia under postarktisk tid. — GFF, 46: 1—2, s. 83—128, 9 fig., pl. 2—4.

Yttrande med anledning av F. Enquists föredrag om sambandet mellan klimat och växtgränser. — GFF, 46: 1—2, s. 211.

Rec. av G. Booberg, En högmosses utvecklingshistoria. — GFF, 46: 3—4, s. 366—367.

1925

»Fyndomständigheter» [tills. m. S. Lindqvist] och »Åldersbestämning». — Ingå i: L. von Post, Emelie von Waltersdorff & S. Lindqvist, Bronsåldersmanteln från Gerumsberget i Västergötland. — K. Vitt. Hist. o. Ant. Akad., Monografiser., 15, s. 9—26, 46—59, 70—71, 5 fig., 1 färgpl.

Gotlands-agen (Cladium Mariscus R. Br.) i Sveriges postarktikum. — Ymer, 45: 3—4, s. 295—312, pl. 15—17.

»Myrar, träsk och vätar» och »Ur den gotländska vegetationens senkvartära historia». — Ingå i: H. Munthe, J. E. Hede & L. von Post, Gotlands geologi. — SGU, Ser. C: 331, s. 77—129, fig. 46—74, pl. 7—9.

Torvmarker. — Ingår i: H. Munthe, J. E. Hede & L. von Post, Beskrivning till kartbladet Ronehamn. — SGU, Ser. Aa: 156, s. 76—83, 3 fig.

Rec. av H. W:son Ahlmann, C. C:zon Caldenius & R. Sandegren, Ragundasjön, en geomorfologisk, geokronologisk och växtgeografisk undersökning. — Fornvännen 1925, s. 86—89.

1926

Einige Aufgaben der regionalen Moorforschung. — SGU, Ser. C: 337 (= Årsbok 19: 4), 41 s., 15 fig.

Medel och mål i skånsk torvmosseforskning. — Sydsvenska Geogr. Sällsk. Årsbok 1926, s. 76—114, 16 fig.

Södra Sveriges torvtillgångar I [tills. m. E. Granlund]. — SGU, Ser. C: 335, 127 s., 54 fig., 15 pl.

1927

Beskrivning till översiktskarta över södra Sveriges myrmarker. — SGU, Ser. Ba: 11, 51 s., 29 fig., 1 karta. [Engelsk upplaga aviserad på titelbladet men ej utgiven.]

Myrmarker. — Ingår i: H. Munthe, J. E. Hede & L. von Post, Beskrivning till kartbladet Hemse. — SGU, Ser. Aa: 164, s. 101—137, 21 fig.

Svea Älv. Ett geologiskt naturminne. — Sveriges Natur 1927, s. 7—31, 9 fig., 2 pl.

Pollenanalyse. — Reallexikon der Vorgeschichte, hrsg. M. Ebert, 10, s. 221—229, pl. 91—95. Berlin 1927—28.

1928

Pollenstatistik. — Naturens liv i ord och bild, utg. L. A. Jägerskiöld & T. Pehrson, 2, s. 612—628, 12 fig. Stockholm.

Svea Älvs geologiska tidsställning. En pollenanalytisk studie i Ancylustidens geografi. — SGU, Ser. C: 347 (= Årsbok 21: 2), 132 s., 24 fig., 2 pl.

Ur den svenska skogens fornhistoria. — Naturens liv i ord och bild, utg. L. A. Jägerskiöld & T. Pehrson, 2, s. 689—711, 14 fig. Stockholm.

1929

Den »postglaciala landsänkningen». — Nord. Tidskr., 5, s. 506—525, 9 fig.

Die Zeichenschrift der Pollenstatistik. — GFF, 51: 4, s. 543—565, 8 fig.

Geologi. — Ingår i: Kunskap. Bonniers universitet för alla, 4, s. 285—371, 130 fig., 1 tab. Stockholm.

»Istiden», »Den varviga leran som tidmätare», »Våra torvmossar», »Jordmånerna», »Värmetider och fimbulvintrar». — Ingå i: I. Sefve, Liv och materia. Läsebok för skola och hem. Andra delen, s. 7—13, 2 fig.; s. 25—32, 4 fig.; s. 46—55, 2 fig.; s. 55—62; och s. 62—70, 1 fig. [andra kapitel rent geologiska (s. 7—80)]. Stockholm.

Kvartära bildningar. — Ingår i: N. H. Magnusson & L. von Post, Beskrivning till kartbladet Säffle. — SGU, Ser. Aa: 167, s. 39—96, 35 fig.

Om Gotlands myrar. — Svenska Mosskulturfören. Tidskr., 43: 1, s. 229—247, 9 fig.

Pollenanalytisk undersökning. — Ingår i: O. Rydbeck & L. von Post, Ornerad skafthålsyxa av hjorthorn funnen i Höganäs. — Fornvännen 1929, s. 141—154, 2 fig.

Svea, Göta och Dana Älvar. — Ymer, 1929: 1, s. 1—33, 20 fig.; sep. med samma titel och tillägget: »jämte marschroute för beseende av Sveafallen vid Degerfors». — Svenska Turistfören. Publ. 452, 37 s., 21 fig. Stockholm.

Vänerbassängens strandlinjer. — GFF, 51: 2, s. 199—235, 12 fig., 1 pl.

Växtfysiognomisk karta öfver Tåkern [tills. m. A. Hannerz och K. E. Sahlström]. — Ingår i: Sjön Tåkerns fauna och flora, utg. K. Svenska Vet. Akad. — Uppsala.

1930

Die postarktische Geschichte der europäischen Wälder nach den vorliegenden Pollendiagrammen. — Verh. Intern. Kongr. forstl. Versuchsanst. (Stockholm 1929), hrsg. S. Petrini, s. 1—27, 15 fig. Stockholm.

Norrländska torvmossestudier. II. Några huvudpunkter i skogens och myrarnas postarktiska historia inom södra Norrland. — GFF, 52: 1, s. 63—90, 6 fig.

Närke. En landskapsskiss. — Svenska Turistfören. Årsskr. 1930, s. 23—55, 27 fig., pl. 13—14.

1931

Diskussionsinlägg om pollenanalys och senkvartär vegetation. — Rept Proc. 5th Intern. Bot. Congr. (Cambridge 1930), s. 69—70 och 71.

Diskussionsinlägg om vegetationskartor. — Ibid., s. 129.

Eldslandets postglaciala klimathistoria. — GFF, 53: 3, s. 373—374.

Pollenanalys. — Nordisk Familjebok, 3. uppl., 15, sp. 1186—1188, 3 fig.

Problems and Working-lines in the Postarctic Forest History of Europe. — Rept Proc. 5th Intern. Bot. Congr. (Cambridge 1930), s. 48—54.

Ur jordklotets saga. — 176 s., 153 fig.; Uppsala (tr. i Stockholm).

1932

Beriktigande. — GFF, 54: 3, s. 375.

1933

A Gothiglacial Transgression of the Sea in South Sweden. — Geogr. Annaler, 15: 2—3, s. 225—254, 16 fig., pl. 9.

Den svenska skogen efter istiden. — Studentfören. Verdandis Småskr., 357, 64 s., 15 fig. Uppsala.

Geologiska Institutets Viskan-undersökning 1932. — GFF, 55: 4, s. 659—662.

On Improvements of the Pollen-analysis Technique. — GFF, 55: 3, s. 523—527.

Ur Europas skogshistoria efter istiden. — Studentfören. Verdandis Småskr., 358, 64 s., 19 fig. Uppsala.

Våra myrar som naturdokument. — Sveriges Natur 1933, s. 7—20, 9 fig.

1934

Bonäslinjen. En lednivå bland Siljansbäckenets senkvartära strandlinjer. — GFF, 56: 1, s. 19—51, 12 fig.

Rec. av R. Nordhagen, De senkvartære klimavekslinger i Nordeuropa og deres betydning for kulturforskningen. — Historisk Tidskr., 54: 1, s. 93—97.

1935

Der Bålen-See und die Bålen-Seestudien. — GFF, 57: 2, s. 302—317, 6 fig.

Die schwedischen Urkunden zur Geschichte des spätquartären Klimas. — Zesde Intern. Bot. Congr. (Amsterdam 1935), Proc., Vol. II, s. 93—95. Leiden.

Markens naturmonument. — Vi och vår natur, s. 27—54, 8 fig. Stockholm.

Myriophyllum alterniflorum D. C. in den Bålen-See-Ablagerungen. — GFF, 57: 3, s. 563—569 [sep.: s. 1—7], 3 fig.

1936

Post-Pleistocene Pollen Diagrams from the Southern Hemisphere. I. New Zealand [tills. m. Lucy M. Cranwell]. — Geogr. Annaler, 1936: 3—4, s. 308—347, 2 fig.

Yttrande med anledning av Ebba Hult De Geers föredrag om datering genom årsringskurvor med exempel från Bulverket i Tingstäde Träsk. — GFF, 58: 3, s. 462—464.

1937

Galtabäckslagunen — Båtfyndens ungefärliga ålder. — Ingår i: Ph. Humbla & L. von Post, Galtabäcksbåten och tidigt båtbyggeri i Norden. — Göteborgs K. Vet. o. Vitt.-Samh. Handl., 5. Följden, Ser. A, 6: 1, s. 107—148, 13 fig.

Svea Älv, Göta Älv och Dana Älv jämte vägvisare för besökande vid Sveafallen. — Svenska Turistfören. Publ. 640, 64 s., 25 fig. (inkl. omsl:s). Stockholm.

The Geographical Survey of Irish Bogs. — Irish Naturalists Jour., 6: 9, s. 210—227, 14 fig. [exempel fr. Sverige].

1938

I utsiktstornet på Mösseberg. — Svenska Turistfören. Små Häften, Västergötland: 1; 8 s., 9 fig. (inkl. omsl:s). Stockholm.

Marken. — Nysunds socken, s. 1—31, 15 fig. Örebro.

Odensjön, Skäralid, Klöva Hallar. — Svenska Turistfören. Små Häften, Skåne: 1; 16 s., 13 fig. (inkl. omsl:s). Stockholm.
Säters Dal. — Ibid., Dalarna: 1; 16 s., 13 fig. (inkl. omsl:s). Stockholm.
Tylösand. En halländsk sandbukt. — Ibid., Halland: 1; 8 s., 11 fig. (inkl. omsl:s). Stockholm.

1939

Der Fund und die pollenanalytische Ermittlung seiner Zeitstellung. — Ingår i: L. von Post, A. Oldeberg & I. Fröman, Ein eisenzeitliches Rad aus dem Filaren-See in Södermanland, Schweden. — K. Vitt. Hist. o. Ant. Akad. Handl., 46: 1, s. 7—29, 4 fig.
Diskussionsinlägg om den pågående klimatändringen och pollenanalysen. — Ymer, 59: 1, s. 78—82.
Lina myr. — GFF, 61: 4, s. 519—524.

1940

Kalkens och solens ö [Gotland]. — Svenska Turistfören. Årsskr. 1940, s. 29—54, 15 fig.

1941

Tag vara på torvmossfynden! — Populär Biol. Revy, 3: 2, s. 3—14, 7 fig.

1942

Yttrande med anledning av M.-B. och S. Florins föredrag om »Degerforstraktens senkvartära nivåförändringshistoria. Några synpunkter på Ancylustidens geografi.» — GFF, 64: 3, s. 359—360.

1944

Pollenstatistiska perspektiv på Jordens klimathistoria. — Ymer, 64: 2, s. 79—113, 14 fig. [Se äv. 1946.]
Yttrande med anledning av S. Florins föredrag om »En ny strandförskjutningskurva för södra Mälardalen. Några data till postglacialtidens klimat- och kulturväxlingar.» — GFF, 66: 1, s. 99—103 [+ 109].

1945

En kodex för klimathistorisk istidsforskning. Med randanteckningar ur svenska synvinklar [Klimahefte d. Geol. Rundschau, 34: 7—8, 1944]. GFF, 67: 1, s. 33—48.
Fagus—Helianthemum i svenska pollenspektra. — GFF, 67: 1, s. 49—53.
Yttrande med anledning av J. Iversens föredrag Neolitiske Skovrydninger i pollenfloristisk Belysning. — GFF, 67: 4, s. 565—567.

1946

The Prospect for Pollen Analysis in the Study of the Earth's Climatic History. — New Phytol., 45: 2, s. 193—217, 13 fig. [översättn. av »Pollenanalytiska perspektiv . . .», 1944].
Trädslagsfördelningen i Sveriges skogar under olika skeden efter istiden. — Kartserie i: Gerard De Geer, Sveriges naturrikedomar, pl. mot s. 332. Stockholm.

Vår fornkultur i naturhistoriens ljus. — Svenska Turistfören. Årsskr. 1946, s. 65—88, 10 fig.

1947

Hallands marina fornstränder. α och ω vid Nordens senkvartära nivåförändringar. — GFF, 69: 3, s. 293—320, pl. V—VI.

Viskadalen. Jökelbädd — havsfjord — bondebygd. — Sveriges Bebyggelse, Landsbygden, Älvsborgs län, Del I, s. 9—30, 6 fig. Stockholm (tr. i Uddevalla).

Viska-undersökningens resultat beträffande senglacialens klimatutveckling och strandytor. — GFF, 69: 2, s. 206—214.

Yttranden med anledning av K. Fægris föredrag Heterodoxe tanker om pollenanalysen. — GFF, 69: 2, s. 232—239, 1 fig., och s. 241.

Yttranden med anledning av M. Sauramos föredrag Metoder och data vid utredandet av de senglaciala nivåförändringarna i Finland. — GFF, 69: 2, s. 205—206.

1950

Rec. av K. Fægri & J. Iversen, Text-book of modern pollen analysis. — GFF, 72: 3, s. 363—364.

SAMMANKOMSTER ÅR 1950.

Botaniska Föreningen i Göteborg.

Den 27 januari.

Dr Harald Fries demonstrerade ett stort antal växter från Bohuslän, insamlade under sommarens exkursioner.

Den 10 mars.

Docent O. Selling, Stockholm, skildrade med tillhjälp av färgbilder vegetationstyper ur Australiens och sydvästra Stilla havets växtvärld.

Den 31 mars.

Notarie G. A. Westfeldt, Borås, talade om sina växtgeografiska studier i södra Västergötland samt visade pressade växter och utbredningskartor.

Den 28 april.

En skriftlig anhållan från prof. C. Skottsberg att bli entledigad från uppdraget att vara föreningens ordförande och ledamot av dess styrelse godkändes och samtidigt beslöt föreningen att kalla honom till hedersledamot.

Lektor R. Sterner talade om »Landskapet och växtvärlden i sydöstra Småland», som illustrerades av ljusbilder och pressade växter.

Den 26 maj.

Dr A. Aleem, Alexandria, höll ett föredrag med titel: »Vegetation of Egypt» och visade ljusbilder.

Den 29 september.

Apot. A. Liljedahl redogjorde för sina försök att utröna var och av vem det av Linné omnämnda Dalslandsexemplaret av *Polystichum Lonchitis* blivit samlat.

Direktör A. Wennerberg demonstrerade av honom insamlade fanerogamer i V. Jämtlands och N. Härjedalens fjälltrakter.

Den 27 oktober.

Fil. mag. Bo Peterson, Stockholm, gav en historik och översikt av Hallands flora och demonstrerade ett antal gamla herbarieexemplar.

Den 24 november.

Till ny ordförande utsågs prof. B. Lindqvist, och till nya styrelseledamöter efter dr Harald Fries och lektor F. Hård av Segerstad valdes lektor R. Sterner och folkskollärare St. Nilsson.

Apot. A. Liljedahl demonstrerade ett engelskt arbete över Storbritanniens ormbunkar, utfört i physiotypi dvs. naturtryck.

Fil. dr Björn Palm, Stockholm, höll ett föredrag med titeln: »Fanerogama parasiter, som jag sett.»

Exkursion.

Föreningens ordinarie vårexkursion företogs den 4 juni med en stor fiskebåt, som dr F. Lindstedt ställt till förfogande, till Torsby sockens skärgård i södra Bohuslän. Först besöktes Särholmen, en mager, starkt fårbetad klippö. Här antecknades *Glyceria maxima* (mycket sällsynt på öarna), *Carex diandra* och *magellanica* samt *Plantago Coronopus*. Därefter ställdes färden till den mera givande Gillholmen med träd- och buskvegetation av bl. a. *Malus silvestris* och *domestica*, *Rhamnus cathartica* och *Crataegus curvisepala*. Här sågs *Viola canina* × *Riviniana* och *Cardamine impatiens* samt *Poa irrigata*. På de vackra strandängarna växte *Ophioglossum*, *Carex recta* och *paleacea*, *Euphrasia tenuis* etc. Ett kortare besök på den lilla Koholmen inbragte *Trollius* (sällsynt på öarna), *Geranium Lucidum*, *Scirpus rufus* och *Carex distans*.

Botaniska Sektionen av Naturvetenskapliga Studentsällskapet i Uppsala.

Den 24 januari.

Till kassaförvaltare för år 1950 valdes amanuens Lars Eric Henriksson och till klubbmästarinna fil. stud. Kerstin Tunelli.

Fil. dr Hedda Nordenskiöld berättade om en resa till U. S. A. och Kanada.

Den 7 februari.

Laborator Axel Nygren höll föredrag: »Formbildning hos arktiska *Poa*-arter.»

Den 21 februari.

Prof. Eric Hultén höll föredrag: »En botanist for till Irland.»

Den 14 mars.

Fil. lic. Rolf Santesson höll föredrag: »Om förekomsten av sporangier och gametangier hos lavgonidier» (autoreferat se nedan) samt fil. lic. Olof Rune: »Om serpentinväxternas ekologi.»

Den 18 april.

Prof. K. Björling höll föredrag: »Betvirus — gulsotens spridningsbiologi.»

Den 10 maj.

Dr A. A. Aleem, Alexandria, höll föredrag: »The Phytogeography of Egypt.»

Den 6 oktober.

Fil. lic. Olov Hedberg valdes till Sektionens ordförande och amanuens Per-Olof Lindahl till sekreterare.

Fil. lic. Rolf Santesson höll föredrag: »Mykosymbios — ett misstolkat förhållande mellan två svampar» (autoreferat se nedan).

Prof. K. V. O. Dahlgren höll föredrag om »Fysiologiska undersökningar över compatibilitetsförhållandena hos ett par heterostyla växter».

Docent G. Lohammar visade levande exemplar av *Spergula maxima* uppdragna ur frö från Finland.

Den 26 oktober.

Till klubbmästarinna valdes fil. stud. Ingegerd Åsgård.

Fil. dr G. Erdtman höll föredrag: »Palynologien och dess kontakter med olika grenar av botaniken särskilt fanerogamsystematiken.»

Den 7 november.

Hölls bokauktion i Sektionens regi.

Den 16 november.

Laborator B. Åberg höll föredrag: »Om auxinantagonister och auxinsynergister i rottillväxten.»

Den 30 november.

Laborator A. Nygren höll föredrag: »Om orsakerna till formbildningen inom *Calamagrostis purpurea*.»

Fil. lic. Olof Rune demonstrerade *Drabata cacuminum* E. Ekm.

Den 5 december.

Prof. E. Melin höll föredrag: »Intryck fran en kongressresa till Brasilien.»

Autoreferat av föredrag hållet på Botaniska Sektionen den 14 mars 1950.

Rolf Santesson: Om förekomsten av sporangier och gametangier hos lavgonidier.

I de flesta botaniska läroböcker och handböcker framhålles såsom en fundamental skillnad mellan de båda komponenterna i en lav, att lavsvampen skulle utbilda självständiga fruktkroppar och egna diasporer medan den symbiontiska algen skulle sakna denna förmåga. Detta är i allmänhet riktigt, men ingalunda en generell sanning.

Hos den tropiska, vanligen barkboende *Coenogonium moniliforme* Tuck. är den symbiontiska algen *Physolinum monilia* (de Wildem.) Printz. Släktet *Physolinum* har ej tidigare påvisats som symbiontisk alg hos nå-

gon lav. I den luckra bålvävnaden hos nämnda *Coenogonium* utbildar *Physolinum monilia* mycket ofta aplanosporangier. Hos samtliga undersökta exemplar av denna lav har aplanosporangier med väl utvecklade aplanosporer påträffats.

Den epifylla, subkutikulärt växande laven *Strigula complanata* (Fée) Mont. har som symbiontisk alg *Cephaleuros virescens* Kunze. Ej sällan påträffar man på bålen av denna lav hårlika bildningar, som brutit igenom kutikulan. Dessa hår bildas av den symbiontiska algen och bestå ofta av en liten grupp zoosporangier (»Hakensporangien»), som sitta på ett skaft av 3—5 långsträckta celler. Hyfer från lavsvampen slingra ej sällan upp runt detta skaft till sporangiehopen i dess topp.

Microtheliopsis Müll. Arg. är ett tropiskt, monotypiskt släkte med *Phycopeltis* som symbiontisk alg. De flesta undersökta exemplar av *Microtheliopsis uleana* Müll. Arg. ha visat sig föra *Phycopeltis expansa* Jennings, men i några fall har *Ph. Treubii* Karst. påträffats. I bålen av *Microtheliopsis* finner man att den symbiontiska algen regelbundet utbildar såväl zoosporangier som gametangier. (Förekomsten av zoosporangier hos denna lav påvisades redan av Vainio 1921, Ann. Acad. Sci. Fenn. A: 15, p. 324.)

(Autoreferat.)

Autoreferat av föredrag hållet på Botaniska Sektionen den 6 oktober 1950.

Rolf Santesson: Mykosymbios — ett misstolkat förhållande mellan två svampar.

Vainio trodde sig 1921 (Ann. Soc. Zool.-Bot. Fenn. Vanamo, 1: 4 p. 56—60) ha påvisat förekomsten av mutualistisk symbios mellan två svampar, *Diplothrix mirabilis* Vain. och *Gonidiomyces socialis* Vain., vilka han samma år på material från Philippinerna beskrivit som nya arter och släkten (Ann. Acad. Sci. Fenn. A: 15, p. 154—155).

En undersökning av dessa båda svampar har emellertid visat att i stället ett typiskt fall av hyperparasitism föreligger och att ifrågavarande svampar ingalunda voro okända tidigare, utan finnas behandlade i den mykologiska litteraturen sedan mitten av 1800-talet. Discomyceten *Diplothrix mirabilis* är identisk med *Calloriopsis herpotricha* (Berk.) R. Sant. nov. comb. [Syn.: *Peziza herpotricha* Berk., Hook. Journ. Bot. 3, 1851, p. 16; *Calloriopsis gelatinosa* (Ellis & Mart.) Syd., Ann Myc. 15, 1917, p. 254.]. *Gonidiomyces socialis* kan ej säkert identifieras på grund av typexemplarets dåliga status, men torde med all sannolikhet vara en art av *Meliola* eller något närstående, hyphopodiat släkte. *Calloriopsis* är en klar parasit på denna sistnämnda svamp.

(Autoreferat.)

Botaniska Sällskapet i Stockholm.

Den 13 februari.

Docent Bertil Kullenberg höll föredrag om »Pollinationsbiologien hos några orkidéer». (Se Sv. Bot. Tidskr. Bd 44. H. 2. 1950.)

Den 27 mars.

Fil. mag. INGMAR FRÖMAN berättade om »Strandhugg på Blå Jungfrun och Stora Karlsö».

Den 25 april.

Fil. lic. OLOF RUNE föreläste »Om floran på nordsvenska serpentinberg».

Den 18 maj.

Vårutflykt till Viksberg och Korpberget i Salem (se Sv. Bot. Tidskr. Bd 44. H. 4. 1950).

Den 8 oktober.

Svamputflykt till Riala socken (se Sv. Bot. Tidskr. Bd 44. H. 4. 1950).

Den 6 november.

Lektor HELGE STENAR höll föredrag om »Några kärlväxter från Tjust».

Den 4 december.

Professor HOLGER ERDTMAN höll föredrag om »Skogens och barrträdens kemi».

Fil. lic. STIG O. PEHRSON och fil. mag. ÅKE S:SON STENIUS demonstrerade Svenska Träforskningsinstitutet.

Till styrelsemedlemmar valdes: professor CARL MALMSTRÖM, ordförande; professor RUDOLF FLORIN, vice ordförande; assistent ERIK SÖDERBERG, sekreterare; agronom ANTON EKSTRÖM, kassör.

Botanistklubben vid Stockholms högskola.

Den 13 februari.

Inför Botaniska Sällskapet, Zoologklubben och Botanistklubben höll docent B. KULLENBERG ett föredrag med titeln: »Pollinationsbiologien hos några orkidéer.»

Den 23 februari.

Professor C. MALMSTRÖM demonstrerade Statens Skogsforskningsanstalt samt talade därefter om »Skogssamhället och dess ekologi».

Den 17 april.

Docent E. RENNERFELT höll ett föredrag om »Rotrötesvampen - en svår skadegörare på våra skogar».

Den 27 april.

Docent T. NORLINDH redogjorde för »En botanisk forskningsresa till Rhodesia».

Den 5 maj.

Docent N. NIELSEN talade om »Mikrobiell framställning av vitaminer, fett och andra ämnen».

Den 28 september.

Fil. dr D. Lihnell demonstrerade Statens Växtskyddsanstalt samt gav en inblick i dess organisation och arbete.

Den 17 oktober.

Till styrelse valdes: fil. stud. Olle Lundkvist (ordf.), fil. kand. Barbro Karlsson (sekr.) samt fil. stud. Anna-Lisa Samuelson (skattm.).

Fil. lic. C. O. Tamm höll ett föredrag med titeln »Något om husmossans näringsekologi».

Den 21 november.

Fil. dr G. Erdtman gav en översikt över palynologiens terminologi, varefter fil. stud. B. Johnsson redogjorde för »Pollenmorfologien hos familjen *Zygophyllaceae*».

Fil. stud. N. Nykvist och fil. stud. G. Wibom visade några färgfotografier från sommarens floristikkurs på Stensund.

Den 12 december.

Lektor K. Afzelius berättade »Minnen från Madagaskar».

Societas pro Fauna et Flora Fennica.

Den 4 februari.

Lärare Martin Ingo, Vasa, föredrog: »Försök med *Elymus arenarius* som näringsväxt.»

I anslutning till föredraget refererade prof. R. Ehrström litteraturuppgifter om användning av frukterna av *Sagittaria sagittifolia* som näringsmedel.

Sedan senaste möte hade av Acta Botanica Fennica utkommit N:o 44: Hans Luther, Vorschlag zu einer ökologischen Grundeinteilung der Hydrophyten.

Ordföranden meddelade, att dr J. Soveri fäst Sällskapets uppmärksamhet vid de betydande hassellundar, som finnas på Gammelgårds ägor i Lampis socken i södra Tavastland. Till gårdens ägare, dr G. Ehrnrooth, hade sänts en av Sällskapets styrelse i dess helhet undertecknad skrivelse, i vilken föreslås fridlysning av åtminstone någon del av dessa lundar.

Prof. T. H. Järvi föredrog en skrivelse från föreningen Vanamo ang. upprättande av vissa forskningsstationer. Till medlemmar i den kommitté, som skall bedriva saken, utsåg Sällskapet för sin del sin ordförande och sin sekreterare.

Mag. Hans Luther delgav Sällskapet iakttagelser över frömognad och groning hos vassen. — Prof. A. Palmgren gav tvenne belägg på vassens spridning genom frön. Prof H. Federley nämnde ett liknande fall från Snappertuna i Nyland.

Forstmästare A. W. Granit redogjorde för observationer rörande de kalla vintrarnas i början av 1940-talet inverkan på växt- och djurvärlden. Meddelandet gav anledning till livlig diskussion.

Inlämnades en avhandling av TH. HERZOG, Jena: »Miscellanea Bryologica II. Paleotropica.» Här beskrivas och avbildas 18 för vetenskapen nya tropiska levermossor.

På dr T. BRANDERS vägnar inlämnades till tryck: »Bidrag till kännedomen om bisamråttans (*Ondatra z. zibethica* L.) kägelbobyggen.» Med fem bilder.

Den 4 mars.

Dr G. EHRNROOTH hade meddelat att Sällskapets önskemål om fredning av lundvegetationen på Gammelgård i Lampis socken kommer att beaktas i den mån gårdens forstligt-ekonomiska intressen sådant tillåta.

Dr GÖRAN BERGMAN föreslog, att Sällskapet måtte skrida till åtgärder för fridlysning av Kytökäringen och Lill-Kytö skär i Esbo yttersta skärgård, Nyland. Fågelbeståndet och vegetationen på skären erbjuda stort intresse. — Styrelsen fick i uppdrag att skrida till nödiga åtgärder.

Mag. H. LUTHER redogjorde i anslutning till de iakttagelser han refererat vid senaste möte för försök över grobarheten hos vassens *(Phragmites communis)* frön.

Doc. HANS BUCH inlämnade till tryck: 1. »*Orthocaulis cavifolius* Buch und S. Arnell, ein für die Wissenschaft neues Lebermoos»; 2. »*Sphenolobus saccatulus* (Lindb.) K. Müll., *Sph. rigidus* (Lindb.) K. Müll. und *Sph. groenlandicus* (Nees) Steph.».

Till tryck inlämnades en avhandling av KARL MÜLLER (Freiburg i. Br.): »Die verwandtschaftlichen Beziehungen der beiden Lebermoose *Scapania glaucocephala* und *S. vexata*.»

Den 1 april.

Fil. mag. fru BRITA SCHWANCK redogjorde för utbredningen av *Hippophaë rhamnoides* i Jakobstads skärgård och inlämnade till tryck: »*Hippophaë rhamnoides* i Om Larsmo kyrkvik.» Föreslog åtgärder för fridlysning av nämnda isolerade växtplats, vartill Sällskapet biföll. — Professor A. PALMGREN lämnade uppgifter om havstornet på Åland.

Den 6 maj.

Sedan senaste möte hade utkommit Acta Botanica Fennica N:o 45: STIG JAATINEN, Bidrag till kännedomen om de åländska sjöarnas strandvegetation, 354 sid., 31 tabeller, 34 fig. och 16 bilder samt 1 karta.

Till tryck inlämnades för apotekare U. WIDLUND: »Förteckning över kärlväxter på Sälskär och Norrskär i Ålands nordvästra skärgård.»

Doc. C. CEDERCREUTZ redogjorde för *Chenopodium*-arternas utbredning i Finland samt inlämnade för tryck: »*Chenopodium urbicum* L. på Åland.»

Dr J. MONTELL hade för tryckning insänt: 1. »Hybriden *Carex Bigelowii* Torr. × *juncella* Fr. i finska Lappland»; 2. »*Agropyron caninum* (L.) PB. var. *glaucescens* Lge × *mutabile* Drob., en för Finlands flora ny hybrid»; 3. »Växtformer från Åland II.»

Årsmötet den 13 maj.

Framlades Memoranda Societatis pro Fauna et Flora Fennica vol. 25,

innehållande förhandlingarna för verksamhetsåret 1948—1949. Volymen hade redigerats av mag. H. Ahlqvist.

Ordföranden meddelade, att Sällskapet vid behandling av nomenklaturfrågor vid sjunde internationella botanistkongressen i Stockholm disponerar över tvenne röster. Prof. A. Palmgren, dr G. Marklund och prof. H. Lindberg fingo i uppdrag att härvid representera Sällskapet.

Dr J. Soveri redogjorde för naturen på Gammelgårdsåsen i Lampis, dit en exkursion var planerad.

Doc. I. Hiitonen inlämnade till tryckning: »Über einige Gartenflüchtlinge und andere Seltenheiten der adventiven Flora Finnlands.»

Den 14 september.

Extra möte. Prof. V. Auer föredrog om istidernas inverkan på floran på Eldslandet och i Patagonien.

Den 7 oktober.

Från trycket hade bl. a. utkommit Acta Botanica Fennica N:o 46: Hans Luther, »Beobachtungen über die fruktifikative Vermehrung von *Phragmites communis* Trin.».

Ordföranden prof. A. Palmgren hade hos Ålands Landskapsnämnd hemställt om åtgärder för fridlysning av Idö jämte det därmed sammanhängande Brunskär i Karlby skärgård i Kökar socken på Åland. Sällskapets styrelse hade i utlåtande till Ålands Landskapsnämnd framhållit betydelsen av förslagets genomförande.

Prof. Harald Lindberg delgav Sällskapet sina intryck från diskussionerna rörande nomenklaturfrågor vid Internationella Botaniska Kongressen i Stockholm sommaren 1950.

Dr A. L. Backman meddelade, att han anträffat levande *Najas flexilis* i mängd i Särkijärvi sjö i Libelits socken i norra Karelen och inlämnade till tryck: »*Najas flexilis* funnen i Libelits.»

Mag. Hans Luther förevisade *Ligusticum scoticum* från Gräsö Örskär i Öregrunds skärgård. Arten är ny för Uppland. Den bör eftersökas även på Finlands sida av Bottenhavet.

Dr H. Törnroth meddelade om fynd av *Juncus macer* i Grankulla, Nyland, samt inlämnade till tryck: »*Juncus macer*, ny för Finland.»

Dr J. Jalas anmälde, att han anträffat *Festuca capillata* i Mariehamn. Arten är ny för Finland.

Prof. A. Palmgren konstaterade i anslutning till föregående, att åtskilliga nya hieracier under det senaste decenniet uppenbarat sig i Mariehamns parker. Det kan eventuellt röra sig om »Parkhieracier», invandrade från Sverige. Föredragaren framhöll betydelsen av att dylika arters utbredning studeras i detalj.

Den 4 november.

Prof. A. Kalela höll ett föredrag om Irlands vegetation och flora.

Prof. E. Reuters Index generalis till Sällskapets fristående skrifter förelåg i tryck. Tomen omfattar 204 sidor. Uppdraget att utarbeta indices

över Sällskapets skrifter gavs åt prof. Reuter år 1935. Nu föreligga 6 tomer omfattande sammanlagt 1 729 sidor. Ordföranden framförde Sällskapets tacksamhet.

Prof. V. Kujala redogjorde för principerna för den tredje linjetaxeringen av Finlands skogar, vilken påbörjas instundande sommar.

Doc. I. Hiitonen demonstrerade några sällsynta adventivväxter från Finland.

Doc. C. Cedercreutz meddelade om en ny lokal för *Rubus arcticus* på Åland.

Den 2 december.

Prof. I. Hustich höll ett föredrag: »Kan jorden föda oss?»

Dr A. L. Backman inlämnade till tryck: »*Najas minor* All. In Europa einst und jetzt.»

Forstmästare A. W. Granit meddelade: 1. »Gynnsam växtperiod för vissa lövträdsgaller»; 2. »Nyttiga björksvampar.»

Dr T. Brander hade insänt bl. a. en uppsats om bisamråttan såsom växtspridare.

Svenska Växtgeografiska Sällskapet.

Den 15 maj.

Sällskapets årsmöte. Styrelsen återvaldes in corpore.

Ordf. hyllade minnet av lektor O. B. Santesson, Uppsala.

Till hedersledamöter valdes prof. Th. Herzog, Jena, prof. L. Hauman, Brüssel, dr R. L. Praeger, Dublin, dr H. L. Shantz, Santa Barbara, Calif., och dr F. Shreve, Tucson, Arizona.

Till korresponderande ledamöter valdes prof. S. Cain, Ann Arbor, Michigan, och dr C. G. G. J. van Steenis, Buitenzorg, Java.

Föredrag av fil. lic. O. Hedberg: »De östafrikanska bergens vegetationsbälten.»

Den 29 november.

Ordf. hyllade minnet av jägmästare E. Andersson, Uppsala, laborator N. Hörner, Uppsala, apotekare K. A. Karsmark, Uppsala, apotekare J. Lybing, Stockholm, soc. stud. P. Sjöquist, Örebro, och lektor J. A. O. Skårman, Stockholm.

Föredrag av dr G. F. Mitchell, Dublin: »The Vegetation of Ireland during the Late-glacial Period.»

Sällskapet har under året utgivit följande band av Acta Phytogeographica Suecica: nr 27, S. Selander, Floristic Phytogeography of South-Western Lule Lappmark (Swedish Lapland) I; nr 28, S. Selander, Floristic Phytogeography etc. II. Kärlväxtfloran i sydvästra Lule Lappmark. (English Summary.)

SVENSKA BOTANISKA FÖRENINGEN.

Årsmötet 1950.

Föreningen sammanträdde den 16 november 1950 å Stockholms högskola, sal 3, under ordförandeskap av professor R. E. Fries.

Ordföranden meddelade, att föreningen sedan föregående sammanträde genom döden förlorat fem av sina medlemmar, nämligen rektor Axel Arrhenius, Örbyhus, lektor Ernst Georg Böös, Göteborg, apotekare Algot Karsmark, Uppsala, apotekare Johan Lybing, Stockholm och lektor Johan Skårman, Stockholm. Ordföranden erinrade om de bortgångnas botaniska gärning och lyste frid över deras minne.

De nya medlemmar, som av styrelsen invalts i föreningen, anmäldes.

Det stadgeenliga valet av funktionärer för år 1951 utföll på följande sätt: till ordförande utsågs professor E. Melin, till vice ordförande professor T. Lagerberg, till sekreterare fil. lic. G. Harling, till redaktör för tidskriften fil. lic. H. Horn af Rantzien, till skattmästare lektor A. Frisendahl, till övriga ledamöter av styrelsen professor R. Florin, lektor I. Holmgren, professor C. Malmström (efter professor R. E. Fries, som undanbett sig återval), professor J. A. Nannfeldt, professor C. Skottsberg, professor M. G. Stålfelt (efter framlidne professor H. Nilsson-Ehle) samt överste C.-A. Torén.

Till medlemmar av redaktionskommittén valdes professorerna G. E. Du Rietz, E. Hultén, T. Lagerberg, C. Malmström, J. A. Nannfeldt och M. G. Stålfelt.

Till revisorer utsågos dr W. Rasch (efter direktör E. Wall, som avböjt återval) och revisor E. Wibom, till revisorssuppleanter agronom A. Ekström och fil. kand. Bo Peterson.

Professor Skottsberg framförde till den avgående styrelseledamoten professor Fries ett varmt tack för dennes mångåriga och gagnerika verksamhet i föreningens tjänst.

Docent Olof H. Selling höll ett med talrika ljusbilder beledsagat föredrag över ämnet: »Australiens växtvärld och dess historiska bakgrund. En översikt.»

Med anledning av föredraget yttrade sig professor Du Rietz och föredragshållaren.

Sammanträdet bevistades av 83 personer.

Nya medlemmar.

Vid styrelsesammanträdet den 26 september 1950 invaldes såsom medlemmar av föreningen: på förslag av assistent E. Söderberg: direktör Clas Herlin, Stockholm och civilingenjör Thomas Ouchterlony, Hägersten; pa förslag av ingenjör P. Olrog: med. dr Eric Kugelberg, Stockholm; på förslag av konservator A. Zander: professor Eleonora Francini, Bari, Italien, docent Ilmari Hiitonen, Helsingfors, herr Erling Johannesson, Hogdals-Nordby, herr Erik K. Johansson, Uppsala och kontorschef Knut Teglöf, Falköping; på förslag av fil. lic. G. Harling: fil. stud. Marianne Albihn, Stockholm, fil. stud. Bo Johnson, Bromma, fil. kand. Barbro Karlsson, Stockholm, fil. stud. Lillolle Lundkvist, Stockholm, fil. stud. Bengt Nyman, Bromma och fil. stud. Anna-Lisa Samuelson, Ektorp. Vid styrelsesammanträdet den 16 november invaldes följande medlemmar: pa förslag av fil. kand. B. Peterson: mr. James Kucyniak, Montreal, Canada; pa förslag av konservator A. Zander: fil. stud. Per Olof Nyman, Norrköping, dipl. agric. Abdel Aziz Mostafa Omar, Shebin El Koam, Egypten, Plant Division, Dept. of Sci. and Industr. Research, Wellington, Nya Zeeland och Istituto Botanico della Università, Milano, Italien.

NOTISER.

Göteborgs högskola. De sakkunniga som tillsatts för att yttra sig om kallelse av prefekten vid Göteborgs botaniska trädgård, fil. dr B. Lindquist, till professor i botanik vid Göteborgs högskola, ha nu avlämnat sina yttranden. De sakkunniga ha varit professorerna G. E. Du Rietz, Uppsala, N. Heribert Nilsson, Lund, J. A. Nannfeldt och H. Osvald, Uppsala.

Doktorsdisputationer. För vinnande av filosofie doktorsgrad försvarade fil. lic. Sigvard Lillieroth den 9 december 1950 vid universitetet i Lund en avhandling »Über Folgen kulturbedingter Wasserstandsenkungen für Makrophyten- und Planktongemeinschaften in seichten Seen des südschwedischen Oligotrophiegebietes» (Acta Limnologica, Bd 3), och fil. lic. Birgitta Norkrans den 12 december 1950 vid universitetet i Uppsala en avhandling »Studies in growth and cellulolytic enzymes of Tricholoma» (Symb. Bot. Ups., XI: 1).

Fysiografiska Sällskapets Linné-pris. 1950 års Linné-pris i botanik har av Kungl. Fysiografiska Sällskapet i Lund utdelats till professor H. Burström, Lund, för hans undersökningar över de högre växternas näringsfysiologi.

Carl Malmström

CARL MALMSTRÖM

60 ÅR

DEN 20 JUNI 1951

Svensk Botanisk Tidskrift. Bd 45, H. 2. 1951.

CHEMICAL COMPOSITION OF BIRCH LEAVES FROM DRAINED MIRE, BOTH FERTILIZED WITH WOOD ASH AND UNFERTILIZED.

BY

CARL OLOF TAMM.

The chemical composition of plants has often been used in agriculture as an indicator of their nutritional status and of the nutrient supply in the soil (See references given by Lundegårdh 1945, Goodall & Gregory 1947, Kitchen 1948). The composition of the plants tested is then compared with that of other plants of the same species which have grown under controlled conditions. This method has often given valuable information regarding the availability of plant nutrients in the soil, information which in many cases can not be obtained from soil analyses.

Several attempts have been made to extend the use of the leaf analysis to forestry, with more or less success (cf. references given by Leyton 1947). Different tree species have different nutrient demands (Mitchell & Chandler 1939) and different abilities to extract nutrients from the soil (Mitchell & Finn 1935), which makes the choice of indicator species very important in studies of forest nutrition by foliar analysis. The variation in composition of evergreen coniferous needles with age and season can be expected to be more complicated than that of deciduous trees, which would make sampling more difficult. This assumption has been supported by preliminary analytical data (Tamm, unpubl.). Of the deciduous trees in Sweden the birch is most common and occurs on the most different types of sites. It is also known that the occurrence and growth of the birch are easily affected by changes in soil nutrient level (O. Tamm 1936; C. O. Tamm 1947). Thus the birch suggests itself as a suitable plant for testing the foliar analysis principle. —

Plants growing on the forest floor, either tree seedlings, shrubs, herbs, grasses or mosses are less suitable, because their composition may vary with the shade beneath the tree stand (cf. Tamm 1950). — A recent paper by Aaltonen (1950), received after this investigation had begun, has confirmed the opinion that the leaf composition of the birch is probably a better indicator than that of spruce or pine.

When the indicator species is chosen, the relationship (if any) between soil nutrient supply and leaf nutrient content must be tested. The obvious way to do this is to make a fertilization experiment. Short-term experiments can be performed with seedlings in pots or field cultures, but there is no certainty that they react in the same way as older trees do in the forest. It was considered that a better way to obtain preliminary information about the value of birch leaf composition as an indicator of soil nutrient supply would be to analyse leaves from already existing fertilized plots. If this test gave a positive result, the correlation between soil nutrient supply, tree growth and leaf nutrient content could be studied more thoroughly in new experiments.

Area investigated. Sampling.

The sites studied comprise two small drained mires, North and South Hällmyren near Robertsfors in Västerbotten, North Sweden. These mires contain fertilized plots, now dominated by birch, and are therefore well suited to an investigation of the fertilization response of this tree. The experiments, which have been described in detail by Malmström (1935, 1943, 1950, cf. also Björkman 1941, 1949), were initiated by the forest officer Wilhelm Ålund.

Both mires were drained in 1910. The vegetation before the draining consisted mainly of *Scirpus caespitosus* communities containing much *Eriophorum vaginatum* and *Andromeda polifolia*; scattered hummocks with pine, *Calluna* and *Sphagnum fuscum* also occurred. After draining, the marginal zones of both mires became wooded, partly with vigorous stands dominated by spruce. Within the central and largest parts of both mires the vegetational changes have been far less pronounced, except on fertilized plots. On N. Hällmyren especially, large areas are now covered by *Andromeda*-lichen heath without trees; where trees occur their growth is very slow. Within S. Hällmyren conditions appear to have been

less extreme. Much of the former *Scirpus caespitosus* community is here replaced by a *Molinia* community (with or without *Andromeda*) or by a very open and slow-growing birch stand.

In 1918 an area of 0.3 ha in the centre of S. Hällmyren was fertilized with 1 metric ton (3.3 t/ha) of wood-ash by Ålund. After an initial luxuriant growth of *Chamaenerion angustifolium* a dense birch stand became established within the fertilized plot. The birches have grown vigorously for 25 years, in sharp contrast to those outside the plot, but now the growth appears to have slowed down in comparison with the younger stand on N. Hällmyren. This stand has grown up after an application in 1926 of 2 tons of wood-ash on a plot of 0.16 ha (12.5 t/ha), and has grown extremely well the whole time after treatment. The average height of the birches was 7.7 m on both plots in 1949, which means that the more rapid growth on N. Hällmyren has already compensated for the difference in age (eight years). No doubt the younger stand will soon surpass the older one in height. All trees within the plots are self-sown and younger than the ash-treatment, with the exception of the few trees (almost exclusively pines) growing on hummocks before fertilization or even draining. The birches dominate, but some pines and spruces also occur within the plots.

Thanks to the activities of Ålund, we are now in possession of invaluable ecological material, which has already supplied important information of scientific and practical value (Malmström 1949, Björkman 1949). From the viewpoint of foliar analysis it is of especial interest that we have here birches on three different levels of nutrition: 1) slow-growing birch shrubs scattered on unfertilized mire, suffering from deficiency in one or more nutrients contained in wood-ash; 2) good birch stand on moderately fertilized plot, now with the growth somewhat checked, probably because of exhaustion of the nutrient supply; 3) vigorously growing birch stand on heavily fertilized plot.

Although our knowledge of the nutrient levels within these areas is only qualitative, leaf samples from them might well serve to substantiate the influence, if any, of ash-application on leaf composition. To investigate this influence leaves were collected from the three areas described above in July, 1949. Within the fertilized plots, branches from the middle of the crowns were cut down with scissors on a pole about 5 m long. Squares 5×5 m were chosen as sampling plots. These squares fit in with the coordinate system

laid out by MALMSTRÖM for mapping the vegetation (see MALMSTRÖM 1935, Figs. 8 and 14), and the coordinates of the NW. corner of each square are given in Table 1 (W.—E. coordinate first). From each square one sample was taken, consisting of leaves from one branch of every tree. Five squares were sampled at N. Hällmyren and six at S. Hällmyren. From the unfertilized parts of the mires samples could only be obtained from individual trees, or rather shrubs, as the birches were mostly very scattered. Samples were taken from each of five birches, growing north-west of the fertilized plot at N. Hällmyren, and ranging from 1.5 to 2.3 m in height. The coordinates of these birches are given in Table 1. — As the birches in the unfertilized area grew with a different light supply and were sampled in a different way from those in fertilized plots, the figures obtained are not strictly comparable. A larger random variation may be expected between samples from individual trees than that between average samples for squares. A more detailed discussion of this and other variations in leaf composition will be given in another paper. — The birches sampled belong to the species *Betula verrucosa* EHRH. and *B. pubescens* EHRH.

The sampling so far described was made in July, 1949. In August, 1950, new samples were collected from the same squares within the ash plots. The intention was in part to get figures on the variation in leaf composition from year to year, but mainly to study the effect of a new application of wood-ash made in the autumn of 1949. Part of the plot on S. Hällmyren was supplied with wood-ash at a rate of 4 t/ha in addition to the 3.3 t/ha given in 1918. Very little difference could be seen in the vegetation of the re-fertilized plot in the summer of 1950, but after leaf-fall the few pines and spruces within the plot showed a marked deep green colour not seen outside the re-fertilized area (MALMSTRÖM, priv. comm.).

Results.

Table I gives the analytical data obtained for both samplings, expressed as per cent dry weight.

Methods. Nitrogen was determined titrimetrically by a micro-KJELDAHL method on duplicate samples. The samples for determination of phosphorus, potassium and calcium were wet-ashed with nitric and perchloric acid. Phosphorus was determined colorimetrically by SCHEEL's method. The potassium determination was made by a flamephotometric

Table I. Chemical composition of birch leaves collected on N. Hällmyren and S. Hällmyren 13.VII.1949 and 19.VIII.1950.

Treatment of area	Coordinates (see text)	% N		% P		% K		% Ca	
		1949	1950	1949	1950	1949	1950	1949	1950
Heavily fertilized in 1926	N. Hällmyren								
	65: 40	2.47	2.37	0.13	0.13	0.48	0.49	0.75	0.94
		2.46	2.39						
	65: 45	2.46	2.41	0.13	0.13	0.46	0.49	0.76	0.96
		2.49	2.45						
	70: 40	2.36	1.69	0.13	0.14	0.51	0.53	0.72	0.99
		2.36	1.71						
	70: 45	2.52	2.48	0.12	0.13	0.51	0.56	0.83	1.02
		2.48	2.50						
	70: 50	2.55	2.55	0.13	0.14	0.55	0.56	0.83	1.17
		2.52	2.54						
	Average	2.47	2.31	0.13	0.13	0.50	0.53	0.78	1.02
Moderately fertilized in 1918	S. Hällmyren								
	95: 65	2.76	2.93	0.11	0.10	0.49	0.55	0.60	0.62
		2.73	2.95						
	95: 60	2.80	2.53	0.09	0.08	0.44	0.45	0.52	0.51
		2.79	2.56						
	80: 75	3.00	2.90	0.09	0.09	0.41	0.46	0.64	0.76
		2.99	2.87						
	80: 80	2.87	2.81	0.09	0.08	0.40	0.43	0.56	0.76
		2.86	2.82						
	Average	2.85	2.80	0.09	0.09	0.42	0.47	0.58	0.68
Moderately fertilized in 1918, re-fertilized in 1949	S. Hällmyren								
	95: 80	2.67	2.99	0.10	0.10	0.40	0.82	0.47	0.80
		2.66	3.03						
	95: 85	2.88	3.17	0.10	0.08	0.41	0.93	0.49	0.87
		2.90	3.19						
	90: 85	—	3.15	—	0.09	—	0.87	—	0.81
			3.17						
	90: 80	—	2.75	—	0.10	—	0.85	—	0.74
			2.76						
	Average	—	3.03	—	0.09	—	0.87	—	0.82

Treatment of area	Coordinates (see text)	% N		% P		% K		% Ca	
		1949	1950	1949	1950	1949	1950	1949	1950
Unfertilized	N. Hällmyren								
	26: 28	1.97	—	0.09	—	0.30	—	0.60	—
		2.00		0.09		0.30		0.64	
	23: 30	2.56	—	0.10	—	0.31	—	0.62	—
		2.56		0.10		0.31		0.63	
	20: 25	1.97	—	0.09	—	0.36	—	0.23	—
		1.93				0.35		0.18	
	18: 23	2.17	—	0.10	—	0.36	—	0.59	—
		2.19		0.10		0.35		0.59	
	22: 16	1.72	—	0.09	—	0.34	—	0.63	—
		1.73		0.09		0.33		0.61	
	Average	2.08	—	0.09	—	0.33	—	0.52	—

method. Calcium was precipitated as oxalate and centrifuged. The precipitate was washed three times with water, dissolved in dilute sulphuric acid and titrated with permanganate (samples taken in 1949); for samples taken in 1950 the precipitate was dissolved in dilute hydrochloric acid without washing and measured flamephotometrically.

The main results can be summarized as follows.

1) As a rule birch leaves collected from the same area in two different years have had a very similar composition. The only consistent trend is an increase in calcium content from 1949 to 1950, which no doubt is entirely due to the later date of sampling. It is well-known that the leaf content of calcium usually increases with the age of a leaf (see for example Mitchell 1936, for birch Tamm 1951 b).

2) The re-fertilized plots form an exception to the statement just given, as far as potassium and calcium contents are concerned. The potassium content of leaves from re-fertilized birches is approximately twice that of leaves from the same birches the year before, and the calcium content is also much increased. Leaf nitrogen and phosphorus do not seem to be affected yet.

3) The contents of phosphorus and calcium have been very nearly the same in leaves from the unfertilized area and in leaves from the plot fertilized with 3.3 ton wood-ash per hectare in 1918. The potassium content was slightly higher in fertilized leaves.

4) A heavy application of wood-ash (12.5 t/ha in 1926) has increased the leaf contents of phosphorus, potassium and calcium significantly in comparison with the contents of leaves from unfertilized or moderately fertilized areas, a difference still notable 24 years after treatment.

5) The nitrogen seems to behave very differently from the mineral nutrients. Nitrogen figures are high on the moderately fertilized plot, low on unfertilized plots and intermediate on the heavily fertilized plot.

Discussion.

1) The good agreement obtained between the samples from the same squares in two different years, and the equally good agreement between similarly treated squares give some support to the view that differences in leaf composition may be a guide to nutritional differences, though more observations are needed on the annual and local variation.

2) The figures from the re-fertilized plots show that potassium and calcium in the wood-ash exert their influence within a short time after application, in contrast to phosphorus. A similar result has been obtained by Romell in a fertilizing experiment on a phosphorus-deficient drained mire on Gotland. Application of phosphoric acid strongly stimulated the growth of the ground vegetation already in the first summer, whereas a similar effect on the wood-ash plots could not be seen before 1 1/2 to 2 years after application (Romell, priv. comm.).

3) Considering the large differences in tree condition between moderately fertilized and unfertilized area, the similarity in mineral nutrient content of birch leaves from both areas may seem surprising. It must be admitted that the two sets of samples are not strictly comparable with regard to light intensity. Leaf samples taken at different elevation on the same tree have differed somewhat in composition, especially in calcium content (Tamm, in prep.), but it can not be decided in what direction this variation might affect the comparison between fertilized and unfertilized birches. — The similar leaf composition found in fertilized and unfertilized birches is, however, fully consistent with Malmström's result (1950) that there is now no appreciable difference in total contents of mineral nutrients in the peat within fertilized and unfertilized parts of S. Hällmyren. Probably the birches have now

used up most of the added nutrients, so that the nutrient level in the soil is no longer high with regard to the most important elements. Of course large amounts of nutrients are supplied to the soil by leaf-fall within the ash-plot, but the competition for these nutrients is very strong, the number of tree roots being much higher within the ash-plot than outside. Observations on mycorrhizal development (BJÖRKMAN 1949 p. 250) also support the conclusion that the available nutrients have been consumed, and that the nutrient level has gradually sunk to a low value.

4) Judging from mycorrhizal development the nutrient level has gradually sunk also within the heavily fertilized plot (BJÖRKMAN l.c.). This process, however, is not nearly so far advanced as on the S. Hällmyren plot. MALMSTRÖM's data (1950) show that the surface peat is considerably richer in mineral nutrients (especially calcium) than the peat from the unfertilized area. The agreement between peat and leaf analysis is thus good, both showing that on the N. Hällmyren plot mineral nutrients still are present in greater amounts than on unfertilized mire or on S. Hällmyren, where growth is checked by nutrient deficiency.

Regarding which nutrients are most important, very little can be concluded from data on plots treated with wood-ash or other complex fertilizers. There is much evidence suggesting general deficiency in mineral nutrients, most pronounced in the case of phosphorus, on many drained mires (MALMSTRÖM 1949 p. 95, cf. BJÖRKMAN 1949 p. 252). Birch leaves from a phosphorus-deficient mire on Gotland (from ROMELL's above-mentioned experiment) have been found to contain approximately the same percentage of phosphorus as those from unfertilized birches on N. Hällmyren (0.08—0.09 per cent P; TAMM 1951 a). It seems well worth investigation whether a minimum level exists for phosphorus in birch leaves, and whether this level is identical with the level found here.

5) From the results of extensive fertilization experiments with wood-ash on drained mires, MALMSTRÖM has concluded that many types of peat, though deficient in mineral nutrients, contain satisfactory amounts of nitrogen for the development of trees (MALMSTRÖM 1949 p. 98). MALMSTRÖM also emphasizes that there occurs nitrogen-deficient peat, usually formed by a *Calluna - Sphagnum fuscum* community, and peat rich in mineral nutrients, e.g. that formed by an alder fen.

Malmström's results have already had great importance for the exploitation of mires by silviculture. Draining enables forest to grow on peat containing satisfactory amounts of mineral nutrients due to soligenous flushing in the past. If the peat is low in nutrients, i.e. wholly or partly of ombrogenous origin, the trees cannot grow without a supply of mineral nutrients either from added fertilizers or, if the peat is shallow, from the mineral subsoil.

Regarding the supply of nitrogen it must be kept in mind that Malmström's results only apply to conditions after draining and especially after fertilization. The leaf data presented here suggest that this supply may be different from the supply of available nitrogen on unfertilized mire — and still more on undrained mire (Tamm, unpubl. data). The unfertilized birches have varying but mostly low nitrogen contents in comparison with the fertilized ones, which suggests a lower nitrogen supply. The nitrogen figures from the unfertilized mire lie within approximately the same range as figures obtained for birches on mineral soil (Aaltonen 1950, Tamm unpubl.), while the fertilized birches contain more nitrogen than most birches from mineral ground.

The high nitrogen figures for leaves from ash-fertilized birches no doubt indicate a high level of available nitrogen within the ash-plots. The higher nitrogen supply on the moderately fertilized plot, compared with that on the heavily fertilized plot, may only be apparent and due to the lower production of plant substance containing nitrogen. But the high nitrogen level within both ash-plots seems to be a consequence of the fertilization. Evidence for the occurrence on the ash-plots of a »mobilization» of nitrogen in the sense of Hesselman has also been obtained by peat analysis by Malmström. Earlier analyses (Malmström 1935) failed to show any difference in nitrogen content between peat samples taken inside the ash-plots, and outside. New data (Malmström 1950) reveal a tendency to lower nitrogen contents within both ash-plots, as compared with outside them. This is most easily explained by assuming that part of the nitrogenous compounds within the fertilized plots have been decomposed, and their nitrogen made available for the birches, which have consumed a large part of it. To prove this theory a computation of the amounts of nitrogen contained in vegetation is most desirable. — It should be emphasized that this mobilization of nitrogen on the ash-fertilized plots is a secondary effect. It is certainly beneficial for the trees, but the

checked growth outside the plots must be caused by deficiency in mineral nutrients, not by lack of available nitrogen.

6) From the viewpoint of leaf analysis the results of this investigation, discussed in connection with the available information concerning tree growth and peat chemistry, are very encouraging, confirming the assumption that birch leaf composition can be a sensitive indicator of site properties. The small differences in mineral nutrient contents between unfertilized and moderately fertilized birches, however, show that leaf composition does not always reflect the absolute amounts of nutrients available per unit area. Due attention must be paid to competition, and leaf composition is perhaps better related to the amounts of nutrients available per unit of living plant substance, or per unit of annual growth.

Summary.

The contents of nitrogen, phosphorus, potassium and calcium in birch leaves from differently treated sites have been investigated. The sites comprise two small mires (N. and S. Hällmyren) near Robertsfors, Västerbotten, North Sweden, whose vegetational development and peat chemistry are well known through the studies of Malmström. Birches on four different levels of nutrition have been sampled: 1) on drained, unfertilized mire 2) on drained mire, moderately fertilized with wood-ash in 1918. 3) on part of the preceding plot, re-fertilized in 1949. 4) on drained mire, heavily fertilized with wood-ash in 1926.

The differences in composition between samples from these different sites are discussed in connection with the information available concerning tree nutrition on these mires. The value of foliar analysis as a method for investigating plant nutrient supply is also considered.

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Svensk Botanisk Tidskrift. Bd 45, H. 2. 1951.

SEEKING AIRBORNE BOTANICAL PARTICLES ABOUT THE NORTH POLES.[1]

BY

NICHOLAS POLUNIN.

Introduction.

Perhaps at the outset some clarification of this title is advisable. The initial words indicate that it will be chiefly a chronicle of exploratory investigations — a search for such pertinent bodies, if any, as might be present in, or at all events obtainable from, the atmosphere by the methods available or devisible for each occasion. The bodies or 'botanical particles' dealt with are chiefly pollen grains, fungal spores, yeasts, Bacteria and their allies, or occasionally other spores or microscopic plant matter, thus excluding obviously dead cellular or other scraps, whether or not they are identifiable, and ignoring a great deal of organic dust or debris of whatever origin. The plurality of 'poles' is in deference to the fact that both the true or geographic North Pole and the Magnetic North Pole were involved in the course of these studies, both being reached and visited, or virtually so — in the case of the geographic pole under winter as well as summer conditions.

Although some bacteriological studies had earlier indicated that the arctic air may be not altogether sterile, the aerobiological investigation of these regions, at least in our wider botanical sense, appears to have commenced only during 1933. In July and August of that year, Colonel Charles A. Lindbergh exposed petrolatum-coated slides to the atmosphere during flights over and about southern and central

[1] From an invitational address prepared for the Seventh International Botanical Congress, Stockholm, Sweden, July 1950, but not delivered owing to governmental restriction. The present material was subsequently released for publication and was presented to the Biology Colloquium of Harvard University, December 15, 1950.

Greenland, especially, during his flight from America to Europe with a view to establishing a Transatlantic air route. The slides were unspecified glass ones kept in special containers, the device being jocularly termed the 'sky hook'; after LINDBERGH's return they were examined by the late Dr. FRED C. MEIER, whose preliminary accounts (MEIER and LINDBERGH 1935, MEIER 1935) indicated that a considerable diversity of microorganisms and spores was represented thereon, some of them showing »definite evidence of having been alive when trapped».

Unfortunately that able and energetic pioneer in aerobiology, Dr. MEIER, was killed in a flying accident before this interesting material could be worked out and the promised detailed account written. His figures (MEIER and LINDBERGH 1935), however, of »Some of the more conspicuous objects found on slide 9» (exposed over Davis Strait at about 3000 feet as LINDBERGH approached West Greenland in about latitude 64° N.) and »trapped above the Arctic Circle on slide 15» (which was exposed off the coast of East Greenland at about 3000 feet around latitude 72° N.) show various fungal spores and hyphae, apparently some unicellular Algae, and pollen grains (which on slide 15 appear to include a Ragweed or closely allied grain). Accordingly I have tried to locate these slides for further examination; but in spite of helpful cooperation from friends in the Smithsonian Institution of Washington and the United States Department of Agriculture, as well as from Mrs. MEIER and others who were interested, the only slides that have turned up were a few loose ones that were supposed to have emanated from these flights but lacked significant data except for two sets of numbers (neither of which tallied with MEIER's report [MEIER and LINDBERGH 1935]) and moreover were uncovered and in a very sorry state. After examining some at McGill University and others with Dr. ROGER P. WODEHOUSE in his laboratory at Pearl River, N. Y., we reluctantly decided that nothing reliable could be attached to them and so returned them to their custodians.

Early in the same year in which LINDBERGH made his exposures over Greenland, etc., I prevailed upon an Oxford colleague, Dr. W. H. Wilkins, to prepare for me suitable nutrient Petri plates and these I took north with me and in several instances exposed on mountain tops just south of the 70th parallel of latitude in Norwegian Lapland under winter conditions, and in other instances exposed in about latitude 80° N. in Spitsbergen during the summer. As recently noted (POLUNIN, PADY and KELLY 1947), »with the protracted travels and

rough treatment which the plates had undergone, and the crudity of the only methods of incubation available in the field, it was felt that the unexpected number of fungal and bacterial colonies observed in some cases after only brief exposure might be due to contaminations, and so no account was published. Indeed, no reliance could be placed on these 'observations', as many of the plates appeared to be far from sterile before exposure, while in others the medium had become hardened through loss of water. However, the attempts are mentioned here as they appear to represent the first (albeit abortive) ones of their kind in the Arctic and already give some suggestion of relatively abundant life in its atmosphere» (but *see* below).

At this stage it seems appropriate to refer briefly to the early arctic bacteriological studies afore-mentioned. The first seems to have been that of Nyström (cf. 1869) who, advised by Pasteur, appears to have demonstrated the presence of Bacteria in the air of Spitsbergen, though from their unusually slow breakdown of broth he concluded them to be, at best, far fewer in number than in temperate regions. The Swedish expedition of 1898 attempted quantitative examinations of arctic air for Bacteria in various parts of Svalbard by filtering it through powdered sugar, a mixture of salt and sugar, and glass-wool as described by Levin (1899). About 1000 litres being run through the filter to take each sample, and all except one of some twenty samples proving free from Bacteria, it was concluded that practically none were present: the exception was a sample taken on board ship »dans le port de Beeren Eiland» (Bear Island), whence three bacterial colonies were developed. Moulds appeared to be little less sparse. Subsequently in the same general region Hesse (cf. 1914), whose work was primarily concerned with sea water and so has been overlooked in the present connection, exposed agar plates to the air and found so few organisms developing as to conclude that the atmosphere thereabouts was practically sterile.

In these and allied circumstances it came to be assumed that the air in the Far North was more or less devoid of microscopic forms of plant life, at all events in a viable state: which made Lindbergh's and Meier's observations (1935), and my own inconclusive (but still perhaps pertinent) ones, all the more surprising. For they indicated a relatively rich and diverse *aeroflora* or at least representation of disseminules, etc. Such was the situation in 1946 when I resumed my arctic explorational activities after the war — and soon came to kicking myself for not being prepared for aerobiological studies, as

I had plentiful airplane facilities. Meanwhile, illuminating work had been carried out to the south (Moulton 1942, Wolf 1943), and already much earlier the likelihood of considerable long-range dissemination involving the Arctic had to be admitted through such observations as those following the eruption of Krakatau in 1883, when some of the identifiable material was carried 'twice around the world' before settling to the earth, and Nansen's suggestions (1897) of polar ice being covered with »dust that hovers in the earth's atmosphere». There are numerous instances known from various parts of the world of dust being transported for hundreds or even thousands of miles, and in sizes often exceeding the smaller plant disseminules. Instances include Africa (Oliver 1945), Australia (Pavia 1947), North America, Asia, and here in Sweden (where dust from the Sahara has been recorded (Walther 1912), and there is no doubt that dust storms can carry microorganisms (Soule 1934) — and in plenty for great distances. Even from observations in the Antarctic, McLean (1918) came to believe that microorganisms were carried thither »on dust-motes» by air currents — a conclusion also subscribed to by Darling and Siple (1941) for other remote parts of that sixth continent.

Northwards to the Magnetic Pole in 1947.

While preparing for a fresh period of exploration and botanical field-work in the Canadian North-west and the Arctic Archipelago, I prevailed upon McGill colleagues to prepare for me sets of sterile nutrient plates and 'Vaselined' slides which I exposed on a series of four flights between the 12th of August and the 5th of September, 1947. These flights are indicated in the accompanying sketch-map (Fig. 1), the approximate positions of exposure of the individual slides being shown by the black blobs on Fig. 2; the Roman numerals in both figures refer to the separate sorties. Of these the first (I) was in a northerly direction at an altitude of around 5000 feet (1524 metres) in a 'Norseman' aircraft from my base-camp situated on an unnamed lake north-west of Great Bear Lake to Langton Bay on the Arctic Ocean coast, and thence in a north-westerly direction to the mouth of the Horton River near Cape Bathurst. The remaining flights were by twin-engined 'Canso' flying-boat, of which no part lay directly ahead of the air outside the co-pilot's seat whence the exposures were made; they extended over about 1500 miles (2400

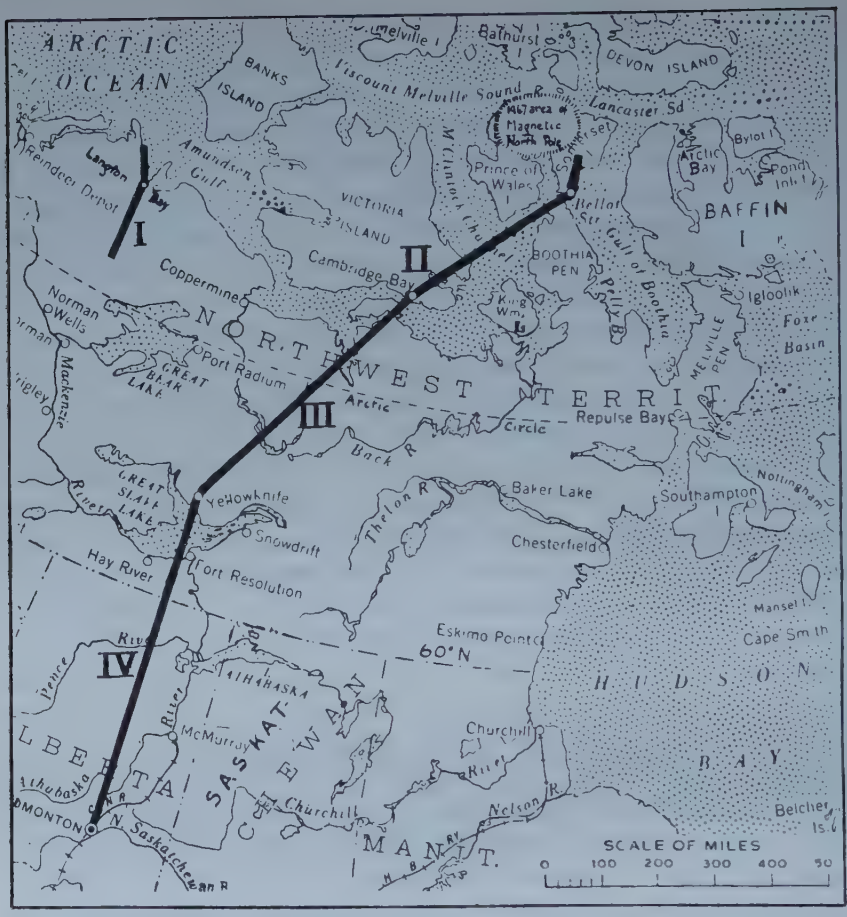

Fig. 1. Aerobiological collecting flights by Nicholas Polunin over northern Canada in July and August, 1947. The Roman numerals refer to the separate sorties mentioned in the text. Courtesy of *Nature* (London).

kilometres) from Somerset Island a little east of (and shortly after a landing virtually on) the Magnetic Pole (situated on Prince of Wales Island) southwards to Edmonton, Alberta, and were made up as follows: (II) on August 26, from Cambridge Bay, Victoria Island, in a north-easterly direction at approximately 4000 feet to the south end of Somerset Island, then northwards until bad weather intervened in about latitude 73° N.; (III) on August 27, from Cambridge Bay in a south-south-westerly direction between 4500 and 7300 feet to Yellowknife, Northwest Territories; (IV) on September 5, at a level

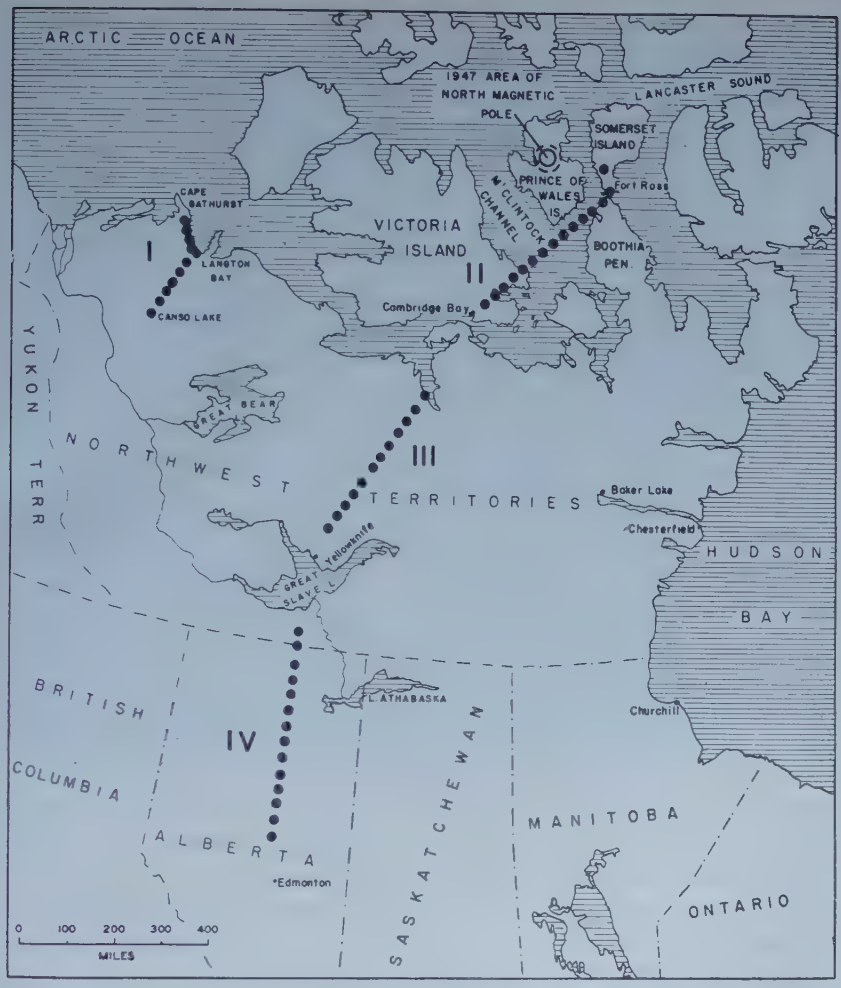

Fig. 2. Exposure of sticky slides on flights indicated in Fig. 1. The Roman numerals again refer to separate sorties and the black blobs to individual slides.

5000 feet from Yellowknife southward to Edmonton. As already described (Polunin, Pady, and Kelly 1947), the airspeed was around 100 knots (115 miles or 184 kilometres per hour) and the medium chiefly employed on the plates, which were ordinary 10 cm. diameter Petri plates and uncovered only in the airstream outside the aircraft, was a modified Czapek's solution containing 2.5 per cent. of agar and with 0.1 per cent. of yeast extract replacing the usual sucrose. I made the exposures by hand, holding each plate with its nearest

point at least 20 cm. away from the fuselage and so that the nutrient surface was struck approximately at right angles by the full force of the airstream for precisely two minutes. During these two minutes a column of air nearly four miles long would of course be traversed. Except for inevitable gaps due to liquid or ice precipitation or preoccupation with landing, etc., a nutrient plate and a sticky slide were exposed either every twenty or every thirty miles, approximately, during the flights concerned (cf. Fig. 2).

The medium on most of the plates having been designed to allow only minimal growth, they were examined at leisure after my return by a bacteriologist, Dr. C. D. Kelly, and a mycologist, Dr. S. M. Pady — with results that have already been described (Pady, Kelly, and Polunin 1948). The outstanding feature of these results was the unexpected range of Fungi and Bacteria that were caught on the plates. Thus whereas we had expected few or no colonies to develop on incubation of the plates that had been exposed in the Far North — for example, over the ice-fields of M'Clintock Channel — we found that almost all on return bore numerous and various colonies of Fungi and Bacteria, indicating both these groups to be plentifully and diversely represented in the arctic atmosphere. As examples it may be noted that the farthest north plate, which was exposed at 4500 feet over Somerset Island in about latitude 72° 38′ N., showed a total of 12 colonies of Fungi and 79 of Bacteria, and plate No. 22, exposed over the sea-ice at 4100 feet not so far to the south-west, showed 6 colonies of Fungi and 95 of Bacteria. Bacteria developed on every plate that had been exposed, the smallest number of colonies being 14 on plate No. 11 which was exposed mainly over the heavy but broken sea-ice of the Arctic Ocean near the coast south of Cape Bathurst. On only one exposed plate did Fungi fail to develop — No. 6, exposed just south of Langton Bay. On the other hand, 7 unexposed plates which were carried throughout these flights proved to be sterile when returned to the laboratory — thus constituting a valuable control. Fig. 3 shows one of the more mycologically productive plates after incubation: No. 9 from about the Arctic Ocean coast in the vicinity of Langton Bay.

In the Arctic and Subarctic, and indeed southward to latitude 58° N. along the route to Edmonton, the bacterial colonies developing on each plate tended to be at least three times as numerous as the fungal ones. North of Yellowknife the only exceptions to this were the afore-mentioned plate No. 11, which had 15 fungal colonies

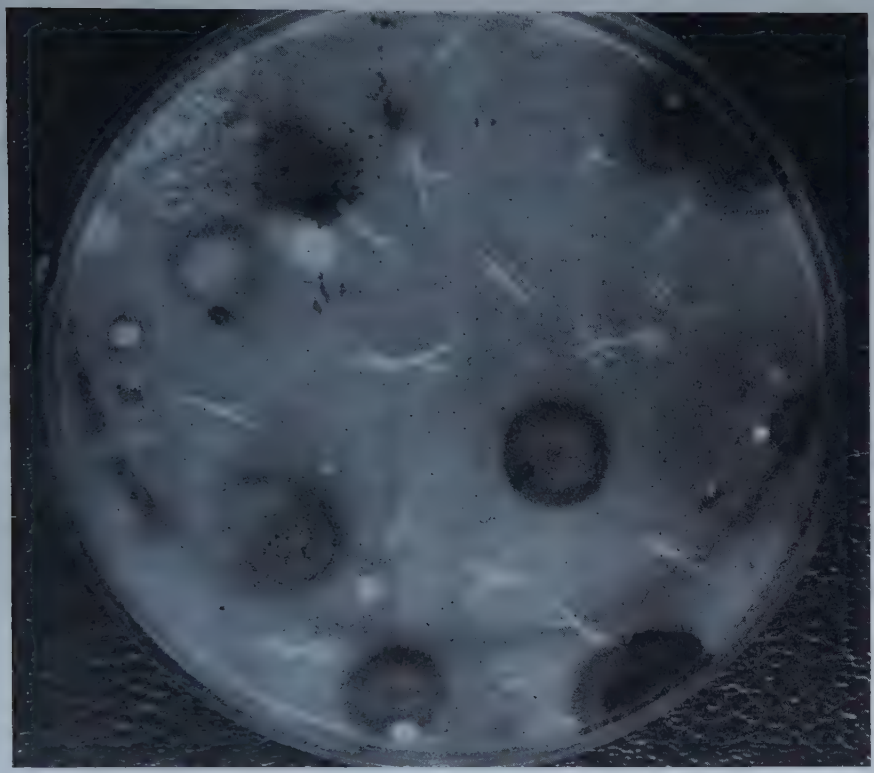

Fig. 3. Petri plate from first sortie of 1947, after incubation. — No. 9, exposed at 5100 feet about the Arctic Ocean coast in the vicinity of Langton Bay, N. W. T., Canada (cf. Fig. 2).

(one more than the bacterial colonies developing) and plate No. 25, which unfortunately was earlier cited (Polunin, Pady, and Kelly 1947) as notable but whose 102 fungal colonies were later determined as being mostly secondary, from a large central one of sporulating *Penicillium* (Pady, Kelly, and Polunin 1948). In the south, however, the discrepancy in Fungi tended to be reduced or even to disappear, the last two exposures over the cultivated region coming in to Edmonton yielding, respectively, 111 Fungi and 62 Bacteria (in the case of plate No. 51) and 306 Fungi and 476 Bacteria (in the case of plate 52). In addition, tiny bacterial colonies were in some cases visible within the fungal mycelia when these were viewed under a dissecting microscope; it was supposed that they »either found the medium to be unfavourable or were inhibited by the fungi. Similarly,

minute fungous colonies were also noted, although much less frequently: two such colonies when transferred to corn meal agar failed to grow» (Pady, Kelly, and Polunin 1948).

As has already been reported (Pady, Kelly, and Polunin 1948), 207 subcultures were made on corn meal agar from the fungal colonies with the following results: Fungi Imperfecti (55) composed of *Hormodendrum* (33), other Moniliales (20), *Phyllosticta* (1), *Pestallozia* (1); Ascomycetes (41) composed of yeasts (16), *Penicillium* (15), *Leptosphaeria* (9), *Chaetomium* (1); Actinomycetales (22, all *Streptomyces*); other cultures (89) composed of non-sporulating (74), sclerotia-producing (2), no growth on transfer (9), contaminated (4). For preliminary identification, also, a total of 188 subcultures were made on nutrient agar slopes from representative bacterial colonies: they comprised *Micrococcus* (43), *Sarcina* (5), *Achromobacter* (probably, 8), *Achromobacter* or *Flavobacterium* (24), Gram-positive rods (unclassified, 20), Gram-positive rods morphologically like *Corynebacterium* (46), spore-formers (8), no growth on transfer (21), mixed cultures (13).

Already from these studies it seemed that, at least on the basis of the colonies which developed in these particular circumstances, living bacterial cells considerably outnumber fungous spores in the arctic air, though to be sure the situation might appear different if there could be studied also the representation of pathogenic and other types which do not culture. Apart from a suggestion in the region of Edmonton that an increase in numbers and diversity of both bacterial and fungal colonies might be directly related to areas of cultivation, there seemed to be little correlation with geographical position. No explanation can be given of the high numbers of bacterial colonies that developed on plates exposed in the vicinity of Cambridge Bay on two successive days, unless they were in part due to the disturbance of unprecedented local construction and other activities and a considerable temporary population at that place, and in part to contamination from my sleeve (the 'sliding' was on my fingers) in the manner suggested by Newman (1948) although in view of the fact that only the rim, at most, of the cover of the Petri plate touched this sleeve and the covers were kept the right way up and wrapped each in its own piece of wax paper within the fuselage during the period of exposure, it seems scarcely conceivable that contaminations from this source could be at all numerous. Also, little if any such effect was noticeable after leaving other places

although the same methods were employed; and finally, the highest total count of all was obtained on the last plate to be exposed, as I came near to Edmonton. In this connection it may be pertinent to quote from a letter received in the autumn of 1949 from Mr. F. C. Bawden, Head of the Department of Plant Pathology, Rothamsted Experimental Station, Harpenden, England, saying that in these results »we found much to interest us. P. H. Gregory is doing a good deal of spore-trapping here, and has compared your catches with his. Accurate comparisons are difficult, but it would seem that, for similar volumes of air, your spore catch is about 1/25,000 of ours. On our standards, the arctic air is free from spores, and any other result would be surprising. Your catches of Bacteria relative to Fungi are much higher than ours.» Meanwhile I should note that a mathematical advisor has computed that under the conditions I described, about 50 per cent. of the spores and similar material in the air should penetrate any cone of relatively static air in front of the plate during flight and so reach the surface of the medium, though what proportion might fail to stick is not known and indeed it must be emphasized that these results are qualitative or at most comparative rather than truly quantitative. It should also be noted that, as far as it is possible to make comparisons bearing in mind these and other limitations, my highest catches seem to indicate a concentration of microorganisms not far removed from some of those reported from temperate and extensively populated regions of the New World (Wolf 1943).

The 'Vaselined' slides exposed at much the same times during these initial aerobiological flights in 1947 were ordinary microscope ones smeared thinly with the adhesive and kept in individual cardboard containers separately wrapped in wax paper which excluded air currents until each was opened and placed, complete with slide, in a special wooden-handled, copper holder in which the sticky surface was exposed against the air-stream for 5 minutes about as far from the fuselage as the nutrient plate. It was then brought in and the container closed, the whole being re-wrapped and secured with rubber bands for transportation. In this state and without reopening, the whole collection was first sent to the Dominion Laboratory of Plant Pathology, Fort Garry, Manitoba, for examination for the spores particularly of pathogenic Fungi which do not culture. The examination was a simple and direct microscopic one of an area of 1100 mm.^{2} of each slide after removal from its container »in

Table I. Pollen grains and spores observed on vaselined

Slide No.	Approximate at first exposure					Pollen grains etc. per slide (doubtful totals in brackets)			
	Time	Airspeed m. p. h.	Lat. N.	Long. W.	Alt. in feet	Angio-sperms	Gymno-sperms	Pterido-phyta	Bryo-phyta
Flight I, from Canso Lake to Cape Bathurst (slides 1—11), August 12. Fair $^{9}/_{10}$ overcast									
1A	18.22	90	67° 38′	127° 08′	2 000 rising	—	—	1	(?5)
2A	18.32	105	67° 58′	126° 53′	5 100	(?1)	—	—	—
3A	18.42	110	68° 12′	126° 28′	5 100	(?2)	—	—	(?2)
4A	18.52	112	68° 32′	126° 05′	5 100	—	—	—	(?1)
5A	19.02	115	68° 54′	126° 02′	5 100	1	—	—	—
6A	19.12	110	69° 06′	125° 43′	5 150	1	1	—	—
7A	19.22	110	69° 24′	125° 40′	5 350	—	—	1	—
8A	20.23	90	circling over pt.		2 000	—	—	1	(?1)
9A	20.33	100	69° 28′	125° 48′	5 100	—	1	—	—
10A	20.43	110	69° 51′	126° 34′	5 100	—	—	—	—
11A	20.53	115	70° 02′	126° 54′	3 500 descdg. to 1 500	1	—	1	(?3)
Flight II, from Cambridge Bay to Somerset Island (slides 13—27), August 26. At start coming from N.N.W. and towards nothern end of flight from N. after									
13A	05.10	113	69° 23′	104° 00′	3 500	1	—	(?1)	—
14A	05.20	109	69° 36′	103° 21′	3 200	—	—	1	—
15A	05.31	115	69° 50′	102° 39′	4 000	(?1)	—	—	—
16A	05.41	115	70° 02′	101° 56′	4 200	(?1)	—	—	—
17A	05.52	115	70° 15′	101° 13′	4 400	—	—	—	—
18A	06.01	116	70° 25′	100° 35′	4 350	—	—	—	—
19A	06.11	115	70° 37′	99° 45′	4 000	—	—	—	—
20A	06.21	115	70° 49′	98° 59′	4 000	—	—	—	—
21A	06.31	116	71° 02′	98° 08′	4 050	1	—	—	(?1)
22A	06.41	116	71° 13′	97° 20′	4 200	—	—	—	—
23A	06.52	116	71° 27′	96° 25′	4 100	—	—	—	—
24A	07.01	117	71° 36′	95° 40′	4 000	1	—	—	—
25A	07.11	121	71° 48′	94° 50′	4 000	—	—	—	—
26A	07.21	121	71° 59′	94° 00′	3 000	—	—	—	—
27A	07.46	115	72° 41′	94° 30′	5 000	—	—	—	(?1)

slides exposed over northern Canada by POLUNIN in 1947.

Identified fungal spores per slide						Remarks and additional information (conditions fair unless indicated)
Stem Rust	Leaf Rust	*Alternaria* spp.	*Helminthosporium* spp.	Smut	Unidentified	
(ceiling 5,000) at start. Air-mass coming from NW. after travelling E. over ocean.						
—	1	2	1 *H. sativum*	—	1	Also 1 *Pleospora* spore and a septate mycelium
1	—	—	1 *H. sativum*	—	1	Septate mycelium
—	—	—	—	—	1	Septate mycelium, branched
—	—	1	2 *H. sativum*	—	—	C. A. V. U.
—	—	—	—	—	—	
—	—	—	—	—	—	
—	—	—	—	—	—	1 ?*Cladosporium* spore
—	—	—	—	1	—	1 ?*Cladosporium* spore. Smut is not a cereal one (possibly of grass)
—	—	—	—	—	2	
—	—	1	—	—	1	Over coast
1	—	—	—	—	3	Sea-ice heavy but much broken
$^{9}/_{10}$ low cloud: high overcast as well. Strong NW. wind on ground; air-mass in south sweeping around from E. In both cases apparently of arctic Canadian origin.						
—	—	—	—	—	3	
—	—	—	—	—	—	
—	—	—	—	—	—	Septate mycelium
—	—	1	—	—	—	In cloud, slide very wet
—	—	—	—	—	—	In cloud, slide damp (iced)
—	—	—	—	—	—	Over sea-ice; bad icing of slide & hand
—	—	—	—	—	—	Clear again; no icing
—	—	1	—	—	—	
—	—	—	—	—	—	Over contin. sea-ice near high dark coast
—	—	—	1 *H. sativum*	—	—	
—	—	—	—	—	—	Cloudy again, especially below
—	—	—	—	—	—	Flying in sun, clear
—	—	—	—	—	1	
—	—	—	—	—	—	Some cloud, slide wet
—	—	—	—	—	—	Dense cloud; turned back

Table I.

Slide No.	Approximate at first exposure					Pollen grains etc. per slide (doubtful totals in brackets)			
	Time	Airspeed m. p. h.	Lat. N.	Long. W.	Alt. in feet	Angio-sperms	Gymno-sperms	Pteridophyta	Bryophyta
Flight III, from Cambridge Bay to Yellowknife (slides 28—39), August 27. Wind west-N.N.W. in north, apparently of arctic Canadian origin,									
28A	09.30	110	66° 56′	108° 02′	4 500	—	—	—	—
29A	09.45	109	66° 38′	108° 30′	4 600	—	—	—	(?1)
30A	10.00	104	66° 16′	109° 03′	7 300	—	—	—	—
31A	10.15	115	65° 56′	109° 30′	6 500	—	—	—	—
32A	10.30	107	65° 35′	110° 00′	6 300	—	—	—	—
33A	10.45	117	65° 16′	110° 25′	6 200	—	—	—	—
34A	11.00	115	64° 55′	110° 55′	6 000	—	—	—	—
35A	11.15	115	64° 35′	111° 23′	5 700	—	1	1	—
36A	11.30	115	64° 14′	111° 47′	5 500	—	—	—	—
37A	11.45	117	63° 55′	112° 12′	5 300	—	—	—	—
38A	12.00	115	63° 36′	112° 40′	5 000	(?1)	—	—	—
39A	12.15	117	63° 18′	113° 10′	4 600	(?1)	—	—	—
Flight IV, from Yellowknife to Edmonton (slides 40–53), September 5. Winds easterly of southern origin (*see* text), in middle of flight coming from									
40A	08.30	115	60° 25′	114° 00′	5 000	2	?1	12	3 (?14)
41A	08.45	115	60° 00′	113° 59′	5 000	(?2)	—	19	1 (?4)
42A	09.00	115	59° 34′	113° 58′	5 000	—	—	6 (?7)	2 (?3)
43A	09.15	115	59° 08′	113° 57′	5 000	(?2)	—	—	—
44A	09.30	115	58° 42′	113° 57′	5 000	—	—	—	—
45A	09.45	117	58° 16′	113° 56′	5 000	—	—	—	—
46A	10.00	116	57° 50′	113° 54′	5 000	1 (?4)	—	1	1 (?3)
47A	10.15	118	57° 25′	113° 53′	5 000	(?2)	—	2	(?9)
48A	10.30	118	57° 00′	113° 52′	5 000	(?1)	—	3	(?9)
49A	10.45	118	56° 32′	113° 51′	5 000	—	2	3 (?4)	(?4)
50A	11.00	118	56° 06′	113° 50′	5 000	(?3)	—	1	3 (?11)
51A	11.15	118	55° 40′	113° 49′	5 000	(?3)	—	1	3 (?5)
52A	11.30	120	55° 14′	113° 49′	5 000	(?1)	—	5	(?5)
53A	11.45	120	54° 48′	113° 48′	5 000	—	1	1	(?2)

(Cont.)

Identified fungal spores per slide						Remarks and additional information (conditions fair unless indicated)
Stem Rust	Leaf Rust	*Alternaria* spp.	*Helminthosporium* spp.	Smut	Unidentified	
erly on ground at start: continuous low cloud but flew above. Air-mass coming from but from NW. towards southern end of flight.						
—	—	—		—	—	
—	—	—	—	—	—	Dense cloud; slide wet
—	—	—	—	—	—	Flying in sun, clear
—	1	—	—	—	—	C. A. V. U.
—	1	—		—	—	
—	—		—	—	—	Cumulus and local haze
—	1	—	—	—	—	
—	—	—	—	—	2	Cloud but no condensation
—	—	—		—		
—	—	3	1 *H. sativum*	—	2	Slight haze only; trees
—	—	—	—	—	—	Fine weather; forest more or less continuous
—	1	—	—	—	1	
for past 12 hours on ground at Yellowknife. Air-mass in north variable but apparently W.N.W. (possibly Alaskan origin), and in South coming from W.						
20	74	—	—	1	18	Freezing precipitation delayed exposure until lat. 60° 25′ N.
23	68	1	—	34	34	Forest patchy, sun visible
4	14	1	—	9	2	1 teliospore of *Puccinia* sp.
—	1	—	—	—	—	Slight haze and overcast; air markedly warmer
—	—	—	—	—	—	C. A. V. U.
1	4	—	—	—	1	High overcast
4	20	—	—	—	3	
4	24	1	—	—	—	C. A. V. U.; conif. forest
3	9	—	1	38	4	Some cultivated plots
4	29	—	1	29	37	Considerable cultivation
4	7	1	—	21	36	
—	14	—	1	10	9	Forest mixed deciduous, often cleared
2	14	4	7	30	80	C. A. V. U.; mixed cultivation & forest
4	11	4	5	2	99	Mostly cult.; few trees

a relatively spore-free chamber and a 22 × 50 mm. cover glass placed on the slide with water as mounting fluid», and was kindly undertaken by Dr. B. Peturson and Mr. G. J. Green. There soon resulted the announcement (Polunin, Pady, and Kelly 1948) that »on some of the slides exposed near the Arctic Ocean coast there are represented spores of three of the most important airborne pathogens of cereal crops of Canada, viz. Wheat Stem-rust (*Puccinia graminis tritici*), Wheat Leaf-rust (*P. rubigo-vera* . . .), and Foot-rot of Barley and Rye (*Helminthosporium sativum*). This is the better part of 1000 miles north of the Peace River region, which is the nearest likely source of supply of any real extent, and would seem to extend remarkably the much-cited 'at least 200 miles' that spores of the first-named important parasite (which alone has caused an estimated loss in western Canada through injury to the Wheat crop of as much as $ 200,000,000 in a single year) are known to have been disseminated».

Following their examination in the 'Rust Research Laboratory', the slides were sent to Dr. Norman W. Radforth of McMaster University, Hamilton, Ontario, for examination for pollen grains and non-fungal spores. Later on, some were further examined by Dr. Roger P. Wodehouse and myself at the Lederle Laboratories, Pearl River, N. Y. Dr. Radforth reported little further material of interest (i.e., beyond what he was able to determine) to be represented at least in a significant manner, so the observations can now be concluded with the offering of the accompanying table (Tab. I) indicating the pertinent fungal spores and pollen grains, etc., found on these slides. These last totalled 52 (No. 12 was missed) and all except the latest to be exposed (No. 53) correspond approximately to the plate of similar number concerning which details have already been published (Pady, Kelly, and Polunin 1948). Indeed each slide and plate normally formed a pair, being exposed either contemporaneously or consecutively according to the type of aircraft, the facilities immediately available, and my other duties and preoccupations; but it should be remembered that although such a pair of exposures was made where possible at least every 30 air miles, the slides were each exposed for 5 minutes during which nearly 10 miles of the atmosphere was traversed and the altitude as well as position and weather could change considerably. Fig. 2 shows the location of each slide exposure, and Fig. 4 shows some of the more significant objects caught and photographed or drawn and the results kindly submitted by Dr. Radforth.

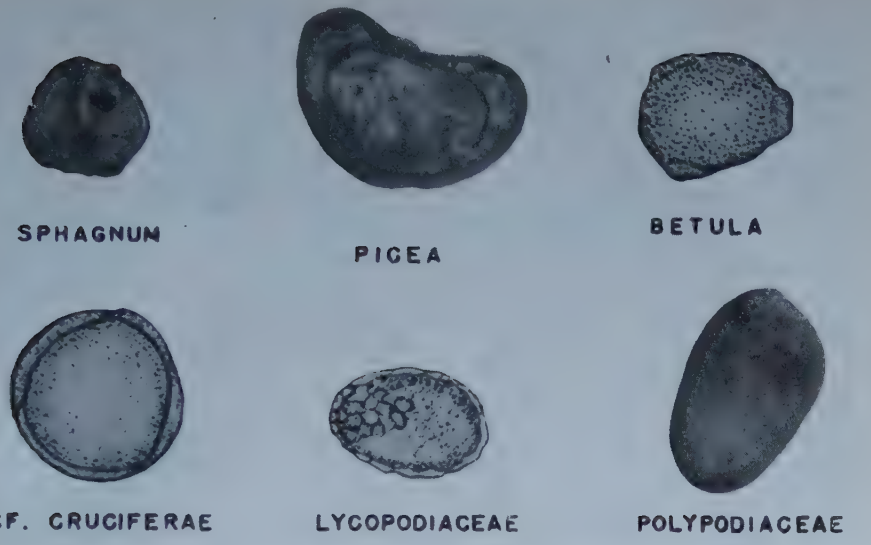

Fig. 4. Some of the pollen grains and spores of cryptogams observed on sticky slides exposed over northern Canada in 1947, during the flights indicated in Fig. 1.

The results of these observations, as indicated in the table, seem sufficiently evident to require no further explanation or emphasis: they clearly confirm the above-mentioned suggestion by Meier and Lindbergh (1935) that pollen grains, etc., are to be found in the atmosphere above remote arctic regions and also the observations by Dyakowska (1948) that 'winged' gymnospermous grains are apt to be involved — as was indeed tentatively suggested as early as 1879 by Wille (1879) to explain his discovery of pollen of *Pinus* among freshwater Algae collected by Kjellman in Novaya Zemlya. Particularly striking is the seeming ubiquity of spores of species of *Helminthosporium* and *Alternaria* (not, of course, necessarily all pathogenic) in the northern air at this season, as well as the occurrence, also sparsely, of those of Rusts and a Smut at fairly high latitudes; in the south, however, these last two groups are relatively abundantly represented — at least according to these limited observations, which are in line with expectations in view of the contemporary infections around Edmonton etc. (Conners and Savile 1948). Similarly there seems no doubt that pollen grains, which have long been known to reach the upper air (Proctor 1934) and to be found over mid-ocean (Erdtman 1937), may in some cases and circumstances be very widely disseminated. The same appears to be true of the spores

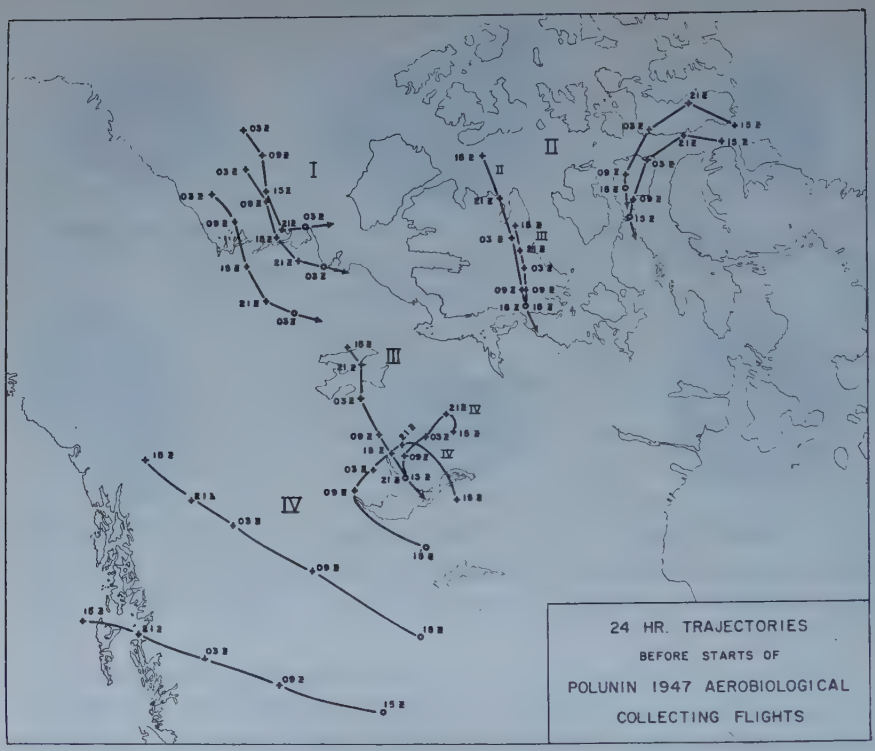

Fig. 5. Trajectories of air-masses in which the four aerobiological flights (indicated by Roman numerals) were made over northern Canada in 1947. In each case the tracing attempts to go backwards for 24 hours before the commencement of the flight concerned.

of Pteridophyta and Bryophyta. Probably a wide range of each of these categories of airborne 'botanical particles' is apt to be involved in this manner. A more detailed account of this phase of the study has been prepared (Polunin, Manuscript 1949). The trajectories of the air-masses in which these four flights were made, for 24 hours before the start of each flight, are indicated in Fig. 5, and are interesting in view of the biota observed, being as highly pertinent as might be expected in the interpretation of their numbers, etc., and seemingly answering the rightful pleas of Persson (1944) and Bergeron (1944).

To the Geographical North Pole in 1948.

In the middle of August, 1948, I was working in Stockholm in the Naturhistoriska Riksmuseum when it was finally confirmed that a

long-planned aerobiological flight over the true, geographical North Pole was going to be possible early the next month. The object was to continue these investigations to the very highest latitudes. So back I went forthwith to Canada, landing at Quebec on the hottest day of the summer, picked up in Montreal my apparatus constructed for the purpose earlier in the year, and was flown by the Royal Canadian Air Force to Ladd A. F. Base, Fairbanks, Alaska, where I was assigned a B-29 (Superfortress) aircraft and special crew of the 72nd (Very Long Range) Reconnaissance Squadron of the United States Air Force. Some days thereafter were spent in preparation and training, with visits for other botanical purposes to Barter Island and Point Barrow on the north coast of Alaska by courtesy of the United States Navy, and on the morning of September 12 we made a partial trial flight during which I had to decide between either continuing to test my apparatus under pressurization at high altitudes or postponing the attempt on the Pole for some days. For weather and other reasons I chose to descend and take off the next morning.

My apparatus, required for exposure of sterile Petri dishes in the unobstructed air-stream in front of an aircraft travelling at around 200 miles per hour, with low temperatures outside and possible pressurization inside, was designed chiefly in collaboration with U. S. Air Force and Navy experts in Washington and constructed on the McGill University campus. It consisted essentially of a steel plate replacing the front large window in the nose, into which a short steel sleeve was welded in a horizontal position so as to surround an opening in the plate that was closed by a sliding door which cut off the outside air. A steel cylinder 68 cm. long and blocked off with a handle at the back, was made to slide within the sleeve; its outside diameter was such that it would hold a 10 cm. Petri dish which rested against a blocking-off metal plate just behind the front end of the cylinder and was held firmly in place by lateral steel clips. Loading was accomplished through a breech cut in the sleeve that had an airtight covering door; for it the cylinder was slid back as shown in Fig. 6 and the sliding door closed (Fig. 7). An unwrapped but still covered, sterile Petri dish was pressed into position in the front end of the cylinder as it lay for loading near the rear of the breech and the cover of the dish was removed, after which the breech was quickly closed, the sliding door opened, and the cylinder slid forward and locked in the exposing position in which the Petri dish was held flat against the airstream about 30 cm. ahead of everything else on

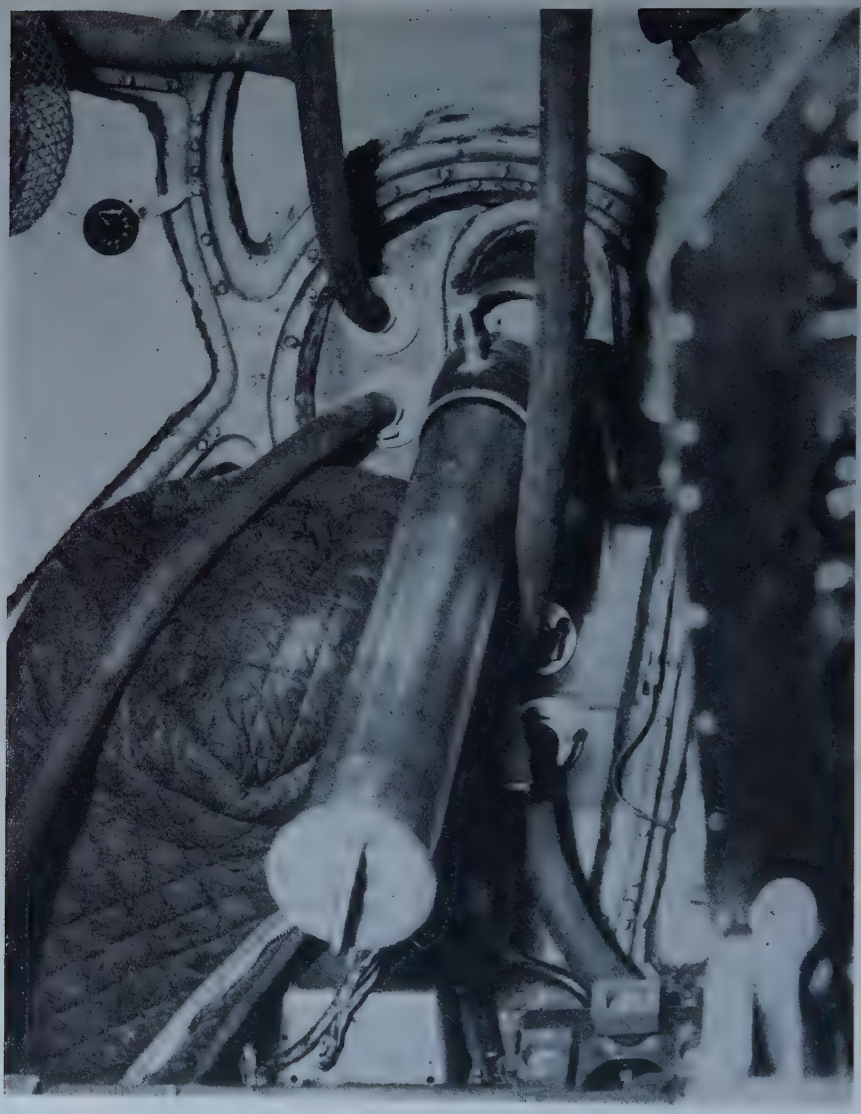

Fig. 6. Interior of nose of B-29 aircraft, looking forward, and showing inner cylinder of aerobiological apparatus drawn back for loading. The breech is open, its airtight flap being visible hanging down on the right. The pairs of tubes seen on either side of this exposing apparatus lead to the vents shown in Fig. 7, and extend back to the filter apparatus and electrostatic sampler shown in Fig. 9.

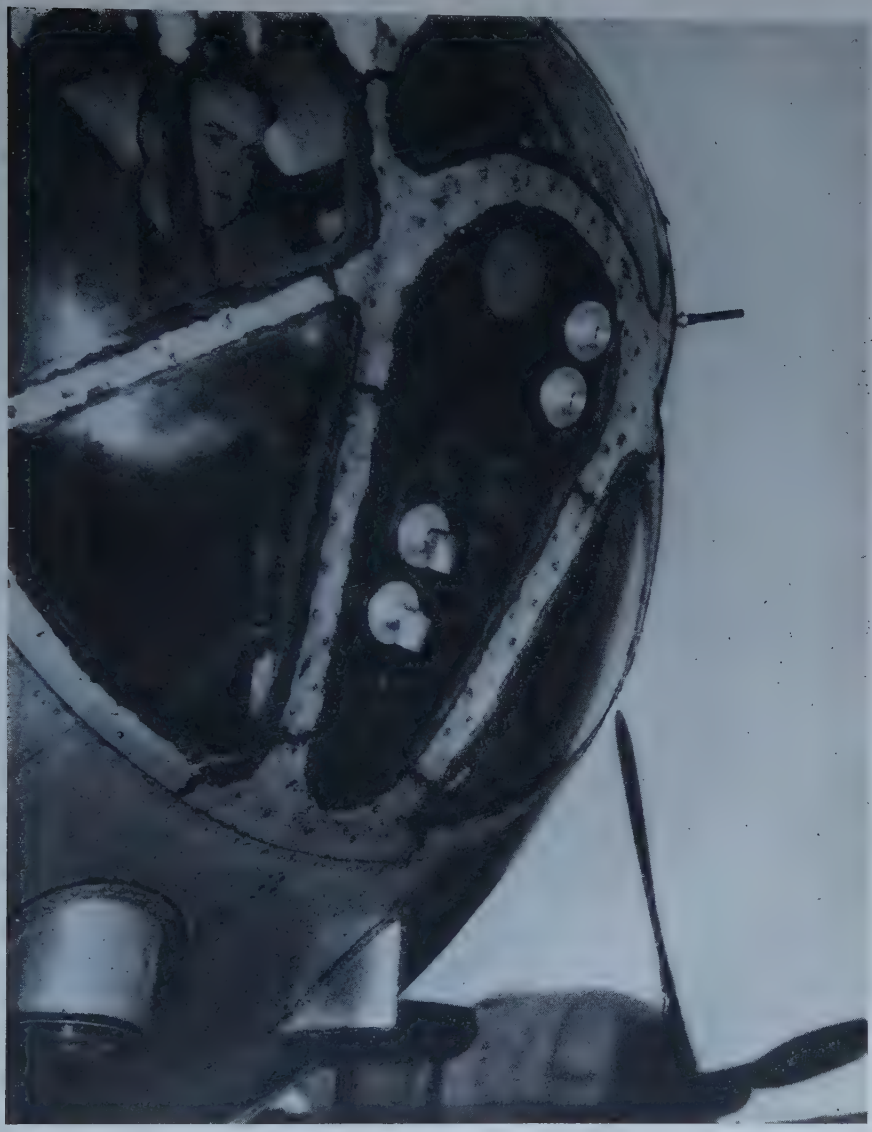

Fig. 7. Exterior of nose of B-29 aircraft with front main 'Plexiglas' window replaced by steel plate perforated to allow protrusion (as in Fig. 8) of steel cylinder holding sterile Petri dish, the cylinder now being withdrawn and the aperture closed by a sliding metal door. Also perforating the steel plate are intake (above) and outlet (below, turned down and slightly back) vents for the filter apparatus and electrostatic sampler seen in Fig. 9.

the aircraft as shown in Fig. 8. Locking was accomplished by a vertical brass plunger which fitted into nicks in the cylinder and had to be done also in an intermediate position owing to the difficulties of manipulation under conditions of high speed and pressurization or oxygen-mask and electrically heated suit and other encumberances which I had throughout that long and arduous flight — not to mention the seemingly innumerable wires connecting me to the crew, power, recorder, and various safety and observing devices. Owing to the low temperatures expected, Vaseline had to be replaced as a 'catching' surface by a smear of silicone grease on the inside of the base of the Petri dish. The silicone employed maintains its stickiness through the remarkable temperature range of —75° C. to over 200° C. and appears to be neutral to most biological activity (Pady and Kelly 1949). Mathematical advice had given the expectation that at least 40 per cent. of the solid particles in the atmosphere would penetrate any air-cushion in front of the Petri plate in flight and be caught on the silicone surface.

The flight of some 4000 miles over the Pole was without mishap, and throughout most of it I loaded and exposed plates for periods of up to 10 minutes each. On return to the laboratory they were 'poured' with melted agar, in which circumstances members of both the fungal and bacterial groups can produce satisfactory colonies (Pady and Kelly 1949). The results are indicated in Tab. II, in which the 'bacterial' colonies are apt to include occasional ones of non-filamentous yeasts; and whereas the counts are mostly so low as to be within the bounds of possible contamination, their grouping and the workings of the controls give confidence in their general validity (Polunin and Kelly, Manuscript 1950). Owing to an unfortunate misunderstanding all of the plates brought back from the first North Pole flight were poured, so no 'dry' microscopic examination for pollen grains etc. was possible.

The main conclusion which it seems safe to draw from these largely preliminary observations is that, whereas the air above and around the North Pole may tend to be practically sterile, it is by no means entirely so. Thus a few Bacteria and very occasional yeasts or other Fungi appear to have been present in a viable condition on this occasion, especially at or slightly above 8700 feet in the vicinity of the Pole itself. The relatively high bacterial counts from the earliest exposures made over central Alaska were not repeated from material obtained on the return flight, although there was still a significant

Fig. 8. Steel cylinder protruded for exposure of Petri plate (shining surface) well in front of everything on B-29 aircraft in flight — cf. Figures 6 and 7.

increase of colonies here (7 on 5 plates exposed for a total of 22 minutes) over the counts made most recently though at the higher altitude of around 18 500 feet farther north (3 on 9 plates exposed for a total of 31 minutes).

Table II. POLUNIN's aerobiological North Pole flight of September 13–14, 1948.

Number	Exposure minutes	Air-speed m.p.h.	Temp. °C.	Altitude feet	Exposure Position		Colonies		Additional Remarks etc.
					Lat. N.	Long. W.	Bacteria[1]	Fungi	
61	1	200	− 8	12 000	66° 50′	150° 18′	30	0	Above cloud; sky clear
62	3	200	− 8	11 700	67° 43′	151° 18′	15	0	
63	5	200	− 8	11 700	68° 00′	151° 35′	28	0	Brooks Range peaks snow-covered; sun rising
64	1	215	− 8	11 000	68° 28′	152° 06′	16	3	
65	3	215	− 8	11 000	68° 42′	152° 26′	1	0	
66	7	200	−10	9 800	69° 16′	153° 10′	0	0	
67	1	200	−10	9 800	69° 47′	153° 55′	1	0	Cloud below complete
68	5	200	−10	9 800	69° 57′	154° 09′	0	0	Icing on wings and slide
69	3	195	−10	9 800	70° 24′	154° 48′	0	0	Plate iced
70	10	195	−10	9 800	70° 36′	155° 15′	1	0	Plate iced
71	3	190	−10	10 500	71° 10′	156° 19′	8	0	Plate heavily iced
72	3	190	−13	10 800	72° 18′	157° 00′	3	0	Plate iced; past Pt. Barrow
73	3	190	−13	10 800	72° 45′	157° 00′	15	1	Clear, so stopped rising
74	10	200	−16	10 800	72° 54′	157° 03′	14	0	Sea-ice broken
75	1	200	−16	10 900	73° 37′	157° 10′	2	0	OK in sun – no more icing
76	5	200	−16	10 900	73° 49′	157° 20′	5	1	
77	3	200	−16	10 900	75° 15′	157° 55′	1[2]	2	Lost plate – and time
78	10	200	−16	10 400	75° 49′	158° 40′	6	1	
79	3	200	−16	10 000	76° 40′	158° 52′	3	0	
80	5	220	−16	10 000	76° 53′	158° 50′	1	0	
81	3	201	−22	8 800	77° 25′	158° 05′	0	0	
82	10	200	−22	8 700	77° 43′	158° 31′	1	0	Still open leads bet. floes
83	1	200	−24	8 700	78° 42′	158° 51′	0	0	Slight haze and icing
84	5	200	−24	8 600	79° 22′	158° 40′	0	0	Sky clear but trace icing
85	3	195	−25	8 500	80° 50′	158° 55′	12	1	Sea-ice almost continuous
86	3	190	−25	8 500	81° 04′	158° 55′	6	0	
87	1	190	−25	8 600	81° 18′	159° 10′	2	0	
88	5	190	−25	8 600	81° 44′	159° 10′	10	0	Few ice crystals on plate
89	10	190	−25	8 600	81° 54′	159° 40′	4	0	Some haze and icing
90	3	190	−23	8 500	84° 18′	162° 00′	7	0	Plate heavily iced; leads of sea-ice frozen over
91	1	190	−21	8 700	84° 40′	162° 30′	4	0	Specks of icing on plate
92	3	190	−21	8 700	84° 52′	162° 30′	6	2	Ice v. irregular about 'pole of inaccessibility'
93	3	190	−21	8 770	85° 06′	163° 00′	2	0	Cloud below

[1] Including very occasional colonies of non-filamentous yeasts.

[2] Gave on culturing 3 yeast colonies.

Table II. (Cont.)

Number	Exposure minutes	Air-speed m.p.h.	Temp. °C.	Altitude feet	Exposure Position		Colonies		Additional Remarks etc.
					Lat. N.	Long.	Bacteria[1]	Fungi	
94	10	190	−21	8 770	85° 17′	163° 00′ W.	11	0	Plate iced over lightly
95	1	190	−18	8 910	88° 10′	161° 00′ W.	7	0	Bad icing; occas. leads frozen
96	1	195	−10	5 000	89° 38′	010° 00′ E.	2	0	Over Pole; icing bad
97	2	200	− 5	3 000	89° 37′	015° 00′ E.	0	0	Icing bad; haze to sea
98	1	200	−15	9 000	88° 58′	172° 00′ E.	1	0	Icing bad
99	2	200	−19	11 500	88° 43′	176° 00′ E.	0	0	Icing still bad
100	2	200	−21	12 750	88° 29′	178° 00′ E.	0	5	Sky clear but some icing
101	1	200	−25	15 000	88° 14′	180° 00′ W.	1	0	Icing less
102	1	198	−27	16 500	88° 00′	180° 00′ W.	1	0	Icing still
103	1	195	−36	18 950	87° 40′	178° 00′ W.	0	0	Icing still; on oxygen
104	1	195	−39	20 000	87° 34′	176° 50′ W.	0	0	Bright sun but still icing
105	1	195	−48	25 000	87° 13′	174° 15′ W.	0	0	Few ice crystals only
106	1	195	−45	23 500	87° 05′	173° 00′ W.	0	0	Very few ice specks only
107	3	195	−42	22 200	86° 40′	171° 40′ W.	1	1	Icing bad; leads frozen
108	1	195	−41	22 000	86° 20′	169° 55′ W.	4	1	Descdg. as engine trouble
109	2	220	−36	18 700	85° 00′	168° 00′ W.	0	0	Navigator passed out
110	5	215	−36	18 700	84° 43′	167° 30′ W.	0	0	Ice specks on plate
111	1	210	−32	18 600	84° 00′	168° 00′ W.	0	0	Bad icing again
112	1	210	−33	18 400	83° 47′	167° 00′ W.	1	0	No precipitation at all
113	3	205	−34	18 350	83° 27′	166° 50′ W.	0	1	
114	10	200	−35	18 500	83° 07′	166° 05′ W.	0	0	
115	1	190	−35	18 600	82° 14′	165° 00′ W.	1	0	Brilliant sun continuing.
116	5	188	−35	18 500	82° 05′	164° 50′ W.	0	0	
117	3	186	−35	18 700	81° 30′	164° 20′ W.	0	0	Sea-ice has open leads
118	1	195	−12	12 300	66° 43′	150° 00′ W.	0	0	Gap (pressurizing etc.)
119	5	203	− 1	10 000	66° 35′	149° 50′ W.	3	0	
120	10	205	+ 4	8 000	66° 02′	149° 00′ W.	0	0	
121	3	207	+ 6	7 000	65° 05′	147° 55′ W.	1	1	
122	3	204	+ 5	5 400	64° 55′	147° 42′ W.	2	0	Circling base to land

[1] Including very occasional colonies of non-filamentous yeasts.

At the highest latitudes, my 21 exposures totalling 44 minutes bore only 18 colonies — possibly because they were mostly made at much higher altitudes of over 18 000 feet, although to be sure a 2-minute exposure made at 3 000 feet as the Pole was circled proved entirely blank. Around 25 000 feet the atmosphere at very high latitudes appeared to be entirely sterile, at least on this occasion — though here again insufficient observations were made for any

definite pronouncement. It has been suggested that the rigorous conditions of very low temperatures and relatively high radiation activity which are apt to be encountered in the upper latitudes and altitudes may have been responsible for the death of organisms, and already in other connections from less unfavourable regions there have been counted by direct microscopic examination many more disseminules than the developing colonies, etc., suggested (KELLY, POLUNIN, and PADY, Manuscript 1950). Actually, however, desiccation at low temperatures is a well-known preservative of life in many microorganisms, and the intensities of total and abiotic radiation tend to be less in the Far North than to the south, altitude for altitude (COBLENTZ, GRACELY, and STAIR 1942), so that in these respects the far-northern atmosphere may favour the preservation of life, even as the strong winds favour long-distance transportation of microscopic bodies carrying the vital spark. Moreover, it is questionable whether conditions even in the stratosphere are widely lethal (MEIER 1936 a).

The North Pole under winter conditions in March 1949.

For comparison of winter conditions with those of the more aestival season giving the results above described, another North Pole flight was carried out in March, 1949. My associates, Drs. C. D. KELLY and S. M. PADY, had meanwhile worked at apparatus and techniques so that this time it was possible to employ three 'catching' systems more or less contemporaneously, viz. (1) the 'artificial hand' used on the previous occasion for exposure in front of the nose except that this time each Petri plate contained two silicone-smeared microscope slides which were stuck with drops of rubber cement side by side on the inside of its base, (2) an »Electrostatic Bacterial Air-sampler» taking two sterile Petri plates at a time and installed in a glass-faced aluminium box (Fig. 9) connected by 1-inch bore rubber tubes (Fig. 6) to vents in the nose of the 'plane (Fig. 7) so arranged as to create a gentle flow of air through the box, and (3) a filter of glass-wool and lens-paper packed in a brass hose coupling and similarly connected with the outside air, except that the outlet led through a flow-meter (cf. Fig. 9) so that a known volume of air was filtered. The sampler employs an electrostatic field of some 6500 to 7000 volts to precipitate airborne particles on the inside surface of the base of the Petri plates, one of which is negatively and the other

Fig. 9. Interior of main forward cabin of B-29 aircraft showing flow-meter installed (above); into this latter on the left at top leads an intake tube in which the brass couplings containing the filters are inserted. The outlet tube is in a similar position on the right. Below is seen the glass-fronted aluminium box containing the electrostatic sampler with, underneath, the top of the vibrator converter. The outlet vent from the box is just visible above the right-hand petri dish in the sampler. The long tubes seen in Fig. 6 connect intakes and outlets with the vents in the nose of the aircraft shown in Figures 7 and 8.

positively charged. A constant volume of 1 cubic foot a minute is so sampled, the air being blown over the sterile agar surface or silicone smear. The filters are of standard thickness and 1 inch diameter and the couplings in which they pack are plugged with

cotton-wool and covered with paper caps for sterilization, being finally wrapped for transportation (KELLY, POLUNIN, and PADY, Manuscript 1950).

With the expectation following the previous flight that the air might be virtually sterile, and now that we supposed 'catching' could proceed even under icing conditions as supercooled water droplets occur rather than ice crystals in clean air down to —41° C. (D'ALBE 1948, A. W. BREWER *voce*), exposures in most cases were made for a full hour on this occasion. Subsequently one of each pair of nose-exposed slides was examined microscopically for pollen grains (after removal from the Petri dish and mounting with glycerine jelly containing basic fuchsin) and the other for fungal spores, the plates from the sampler were 'poured' and incubated, and the filters shaken with sterile water for removal of their entrapped biota which were then grown on agar (POLUNIN and KELLY, Manuscript 1950). The results of an aborted mission on March 28 and of a successful polar flight starting the following day are given in Tab. III. Controls with the artificial hand were practiced as on the previous occasion and proved to be entirely blank as regards pollen grains, etc., as did unexposed slides and several that had been exposed for periods of up to 7 minutes at various stages. One, however, exposed for 7 minutes as we turned around the Pole at an altitude of 5800 feet, remarkably enough proved to have, upon the first slide examined, a Ragweed or closely allied pollen grain and a Smut or allied fungal spore, and, on the other, two spores apparently of *Cladosporium*. Although these may have been contaminations, it is thought that they probably represent valid observations of spores actually trapped over the North Pole (POLUNIN, Manuscript 1950); but it is not known whether they were alive or dead when caught. Nevertheless the chief conclusion to be drawn from these results is that the air at high latitudes in winter may be virtually sterile — as was perhaps to be expected in view of the great distances disseminules would normally have to travel when frozen conditions prevailed and snow covered most areas for 2000 miles or more southward from the Pole.

On the polar flight the only figures that approached the higher ones of the abort were either from exposures made in the south near the beginning, when we may quite likely have been flying in air of relatively favourable origin, or at the highest latitudes, where the air was much mixed and where the above-mentioned pollen grain and fungal spores appear to have been trapped. Another interesting

Table III. Abortive (Nos. 224–242) and North Pole (Nos. 243–289) flights, March 1949.

Number	Type[1] (method)	Air-speed m.p.h.	Temp. °C.	Approx. at exposure			Colonies per cu. ft.		Fungous spores	Pollen grains
				Feet	Lat. N.	Long. W.	Bacteria[2]	Fungi		
224	sampler	189	−30	13 100	66° 07′	148° 55′	0.3	0.06		
225	filter						0.49	0.06		
226	slide[3]								0	0
227	control									
228	sampler	213	−30	13 100	69° 25′	153° 21′	0.23	0.03		
229	filter						0.84	0.00		
230	slide								0	0
231	sampler	217	−26	11 100	71° 46′	157° 10′	0.16	0 00		
232	filter						3.77	0.02		
233	slide								0	?1
234	sampler	199	−25	10 000	74° 54′	155° 48′	0.6	0.00		
235	filter						5.99	0.04		
236	slide								1	1
237	abort									
238	abort									
239	slide	199	−25	10 000	72° 00′	157° 25′			0	0
240	sampler	199	−24	10 100	68° 45′	153° 21′	0.16	0.00		
241	filter						2.19	0.00		
242	slide								0	0
243	sampler	218	−28	13 500	67° 10′	151° 20′	0.2	0.00		
244	filter						2.4	0.21		
245	control									
246	slide								1	0
247	sampler	211	−30	13 500	70° 45′	155° 30′	0.13	0.03		
248	filter						1.4	0.00		
249	slide								2	0
250	sampler	214	−31	13 300	73° 41′	156° 45′	0.03	0.00		
251	filter						(incl. in no. 248)			
252	slide								1	0
253	sampler	204	−31	13 300	77° 20′	160° 40′	0.06	0.00		
254	filter						0.43	0.05		
255	slide								2	0

[1] Exposures normally for 1 hour each; times often staggered and so precise positions and other details may vary.

[2] Including very occasional non-filamentous yeasts.

[3] Each exposure comprised a pair of which one was read for fungous spores and the other for pollen grains etc.

Table III. (Cont.)

Number	Type[1] (method)	Air-speed m.p.h.	Temp. °C.	Approx. at exposure			Colonies per cu. ft.		Fungous spores	Pollen grains
				Feet	Lat. N.	Long. W.	Bacteria[2]	Fungi		
256	sampler	204	−31	13 300	80° 41′	160° 00′	0.1	0.00		
257	filter						0.27	0.04		
258	slide[3]								2	0
259	abort									
260	sampler	210	−31	13 200	84° 25′	162° 00′	0.2	0.00		
261	filter						0.61	0.1		
262	slide								0	0
263	sampler	204	−31	13 300	87° 15′	147° 00′	0.06	0.00		
264	filter						1.3	0.06		
265	slide								0	0
Extra slide exposed for 7 minutes over North Pole — *see* text for results									+	+
266	sampler	204	−25	5 800	89° 00′	155° 00′	0.06	0.00		
267	filter						1.53	0.26		
268	control									
269	slide								1	0
270	sampler	185	−25	5 800	85° 55′	145° 00′	0.23	0.00		
271	filter						0.46	0.07		
272	slide								1	0
273	sampler	168	−25	5 900	80° 35′	156° 30′	0.23	0.00		
274	filter						0.78	0.13		
275	slide								0	0
276	sampler	172	−25	5 300	76° 44′	155° 04′	0.4	0.16		
277	filter						0.2	0.18		
278	slide								0	0
279	sampler	172	−23	5 700	73° 40′	154° 00′	0.1	0.00		
280	filter						0.1	0.03		
281	slide								4	2
282	sampler	200	−26	10 500	70° 30′	154° 30′	0.23	0.00		
283	filter						0.08	0.01		
284	slide								2	0
285	control									
286	sampler	210	−30	12 100	67° 40′	151° 00′	0.23	0.00		
287	filter						0.22	0.14		
288	slide								0	0
289	slide								0	0

[1] Exposures normally for 1 hour each; times often staggered and so precise positions and other details may vary.

[2] Including very occasional non-filamentous yeasts.

[3] Each exposure comprised a pair of which one was read for fungous spores and the other for pollen grains etc.

pair of slides from these flights was No. 281, one of which bore the largest number of fungal spores so observed while the other was the only slide seen to have more than a single pollen grain upon it; exposure was about the north coast of Alaska where there may have been a mixing of air of a relatively southern origin.

Some further observations, tentative conclusions, and plans.

By sticking two silicone-smeared glass slides onto the bottom of a Petri dish, the electrostatic sampler previously mentioned can be made to gather material for direct microscopical examination, following removal of the slides and mounting or other treatment — e.g. for pollen grains in one case and fungous spores in the other. By a simple calculation based on the time of operation and the proportion of the area of the inside of the bottom of the Petri dish that is occupied by the area of slide examined, on recalling that there are positively and negatively charged dishes, each of which repels similarly charged particles, the number of any particular type of 'significant object' in a cubic foot of air can be approximately determined. This may prove a valuable procedure in future, and has been adopted on my Transatlantic flights of 1950. Meanwhile slides so exposed for one hour each by my associates on flights made on 19 July, 1949, from Winnipeg to Churchill, Manitoba, and later from Baker Lake, Keewatin, southward to Churchill, gave the following results, the positive and negative slides being 'lumped': on the former 'leg' from 52° 50′ N. northward to about 55° N. latitude, 2 winged pollen grains of Abietineae, a furrowed grain possibly of *Quercus*, two grains of *Betula* type and one apparently belonging to the Gramineae, with, in addition, 2 spores of *Cladosporium* and 2 of *Alternaria;* on the latter 'leg' from 63° 48′ N. to 61° 25′ N. latitude, 4 pollen grains of *Betula* type (three of them almost certainly of *Betula* itself), 2 (and possibly a third) of Gramineae, and 1 possibly of *Salix*, with a few fungous spores. This latter exposure was entirely over arctic terrain, the former being over the boreal zone, while other exposures between Montreal and Winnipeg tended to bear more various grains and more numerous fungal spores. The air-mass sources are indicated in Fig. 10 and in a general way support the suggestion previously advanced of correlation with observed aerobiota (Polunin, Manuscripts 1949 and 1950).

As indicated in a previous report to the Defence Research Board

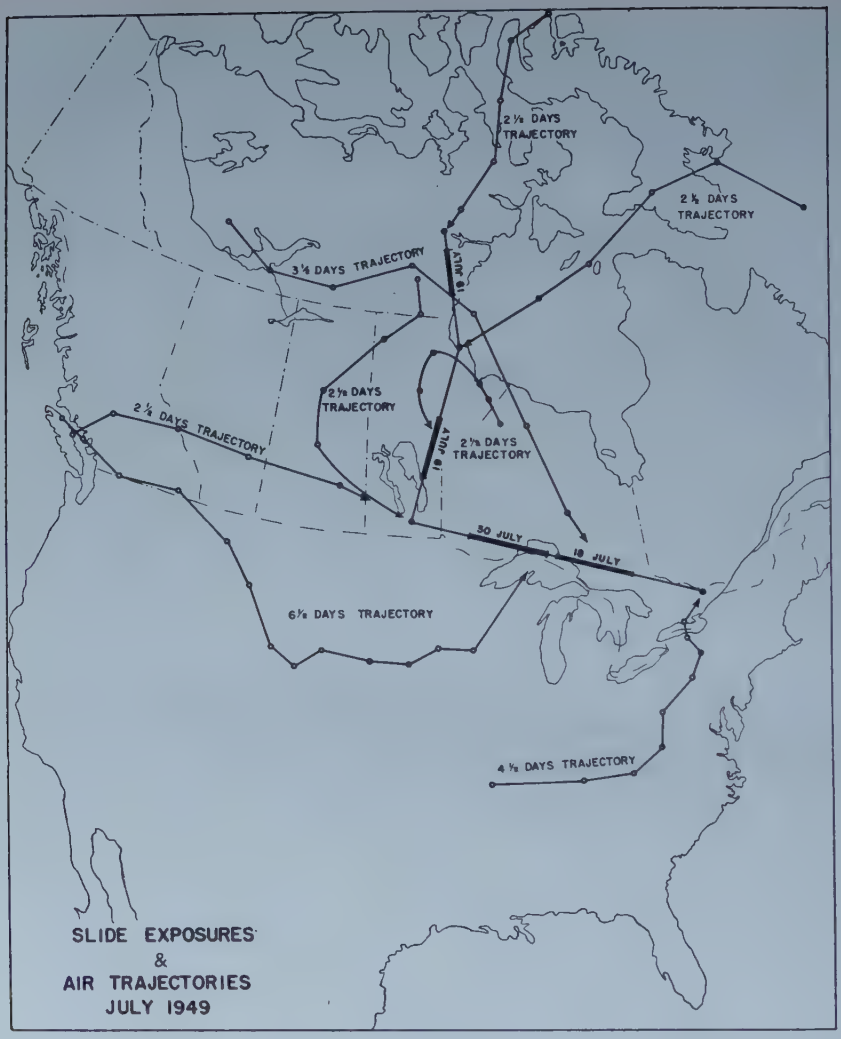

Fig. 10. Slide catchings (indicated by thick lines) and the trajectories of the air-masses in which they were made, traced back from the times of commencement of flights in central Canada northwards to Baker Lake in July 1949.

of Canada, it appears that whereas viable Bacteria tend to outnumber Fungi in the Far North, the reverse is the case in the south, though the reason for this has not been determined. It may lie in part in the proximity of regions of cultivation, but, in view of the manner in which the bacterial numbers are maintained, seems more likely to be due to a quicker 'dropping out' of the larger fungal spores. In

this connection the following figures for colonies developing per cubic foot of air, tested by Drs. KELLY and PADY and their assistants working on this project for which I was responsible, are pertinent and may be compared with others given previously: *July 1949* Ottawa to Winnipeg 0.91 Bacteria and 5.16 Fungi, Winnipeg to Churchill 0.35 Bacteria and 0.47 Fungi, Churchill to Baker Lake and back 4.2 Bacteria and 2.86 Fungi, about Churchill 0.79 Bacteria and 0.78 Fungi, Winnipeg to Montreal 0.45 Bacteria and 1.31 Fungi; *August 1949* Montreal to Winnipeg 0.55 Bacteria and 2.45 Fungi, Winnipeg to Edmonton 1.36 Bacteria and 12.90 Fungi, Edmonton to Whitehorse and back 0.46 Bacteria and 1.27 Fungi, Edmonton to Winnipeg 0.68 Bacteria and 7.34 Fungi, Winnipeg to Ottawa 0.94 Bacteria and 5.60 Fungi. Perusal of these figures and others given elsewhere suggests that biota are not necessarily less numerous in the atmosphere in the north than farther south, although this tends in general to be the case.

Even if the Bacteria tend to outnumber other groups in the atmosphere above truly arctic regions, or at least to afford the most numerous living forms there, they are represented by much the same (usually common soil) types as in the south. It seems likely that they chiefly get into the middle and upper air in the sweeping winds and upward warm eddies rising from southern or at least temperate plains and, although they may be still plentiful in the atmosphere over more boreal regions, that they tend to disappear by gravitational sedimentation or removal by precipitation or death with the long-term circulation or rigorous conditions farther north, even though their corporal flight may be favoured by perpetual windiness and low precipitation in the real Arctic should they get there. Thus there are relatively few viable Bacteria in arctic and polar air especially in winter, although there appear to be some, and with Fungi the situation seems in several ways to be comparable even if they tend to disappear more quickly to the north, although it may be expected that with their number and diversity on the ground in the Arctic, to which not a few forms appear to be largely confined, there may conceivably be some distinctive fungal elements in the arctic atmosphere. More detailed observations will be necessary to determine this, and indicate whether there is indeed such a study as arctic aeromycology. A similar possible localization may prove to exist among pollen grains and the spores of Fungi parasitic on arctic plants of no matter what affinity. With these usually larger and often highly

distinctive bodies, it may moreover be recalled that the direct observation employed ensures, *inter alia*, the preclusion of a possible masking of features by non-development of colonies on unsuitable media. It also makes possible the recording of dead spores and of those of pathogens which do not culture. As is to be expected, all groups tend to be better represented both in variety and numbers in summer than in winter, both in the Far North and over the Prairies.

It should be emphasized that, so far, there have been investigated only a few fortuitous samplings allowing indulgence in a few tentative conclusions which have often been rendered unworthy of projection into generalizations by 'patchiness' of the results. Nevertheless, it seems reasonable to suggest the possibility of some long-distance pollination and hence »absent-treatment» hybridization in the Arctic (Polunin, Manuscript 1950), with prevailing high winds for transportation, and, for survival, low temperatures, low radiation intensities, and low precipitation (rain showers are remarkably effective in removing spores, etc., from the air, cf. Meier 1936 b); resultant long-distance 'genetic' dispersal by hybridization following pollen transportation which can apparently be almost limitless, in view of the well known capacity of some grains to remain viable for many months under suitable conditions, may conceivably be one of the factors behind the notorious plasticity of many groups of arctic angiosperms including, particularly, the Gramineae, Cyperaceae, Juncaceae, Salicaceae, Cruciferae, Rosaceae, and Compositae. A single flying grain finding its stigmatic billet in a millenium might suffice to transport, for example, subspecific characters, and in this connection even wider possibilities spring to mind where the lower plants are concerned, for in their case are transported potential individuals and hence colonies rather than merely potential gametes. It is hoped that studies which are now proceeding in, or concern, very various and widespread arctic and boreal lands and over the water and ice will help in the elucidation of such points and meanwhile indicate something of the pollen and other spore dissemination-patern of those regions through the summer.

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Svensk Botanisk Tidskrift. Bd 45, H. 2. 1951.

ON THE »TRICOLPORITES PROTRUDENS PROBLEM».

BY

G. ERDTMAN.

Tricolporites protrudens (Fig. 1 A) and a number of morphologically ± related pollen types (cf. Fries and Ross 1950, Ross 1949) have frequently been encountered in Upper Cretaceous and Palaeocene strata (stray allochtonous grains have also been found in Late Glacial sediments, etc.). Thus the »*Tricolporites protrudens* flora» probably once formed a significant part of the vegetation in Northern and Central Europe. The systematic position of the possibly ± heterogeneous *Tricolporites* flora is however still unknown.

In a study of pollen grains in approximately 10 000 modern species [cf. G. Erdtman: Pollen Morphology and Plant Taxonomy. Vol. I (in print)] no pollen grains more similar to *Tricolporites protrudens* (and morphologically ± related pollen grains) than those in *Faramea* (Fig. 1 E—G) have been found.

Faramea is a large rubiaceous genus of small trees chiefly restricted to tropical South America. Together with the closely related genus *Coussarea* it forms a distinct tribe, Coussareae, of the subfamily Cinchonoideae. The pollen grains (20 species in all have been investigated) are porate or colporate [brevicolpate; provided with (2—) 3 (—4), exceptionally 5 or 6 apertures], oblate—suboblate (diameter about 25 –40 μ). For sclerine stratification and sculptine details, see Fig. 1 E—G. It should be noted that the bacula in some species of *Faramea* are arranged in a most characteristic manner: in an optical equatorial cross-section all bacula in a mesocolpium are ± parallel to each other and thus not at right angles throughout to the nexine surface. Except in *Faramea* spp. this arrangement has been observed only in some specimens of *Tricolporites protrudens* and ± similar sporomorphs. [The term mesocolpium, proposed

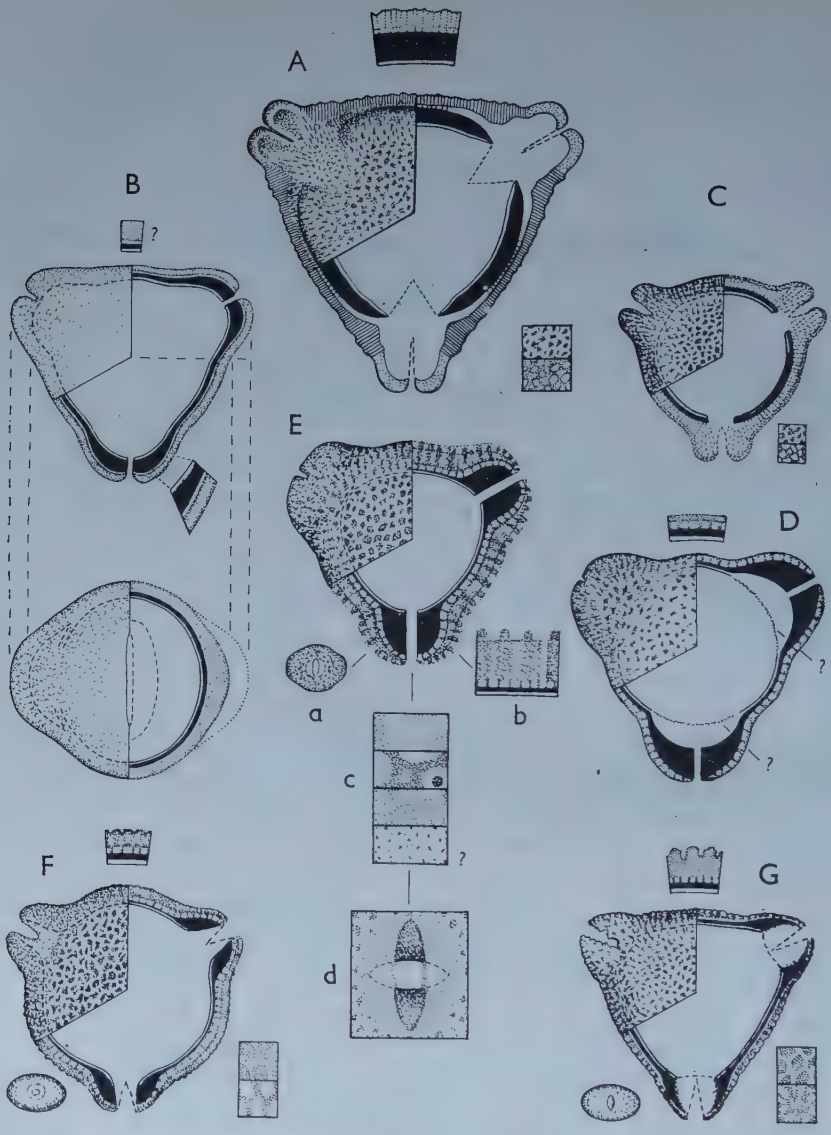

Fig. 1. »Palynograms» of *Farameæ* (E—G) and fossil, ± farameoid pollen grains (A—D). The term palynogram was used in a letter (Dec. 4, 1950) from Dr. W. KLAUS, Vienna, to the present author. After agreement with Dr. KLAUS it is herewith proposed and applied in another sense than the original, viz. as designation of pollen and spore illustrations made in a special, uniform way in order to provide information on polarity, symmetry, apertures, shape, size, sclerine stratification, sexine patterns, etc. (cf. the modern geological term »tectonogram»). — A: *Tricolporites protrudens* ERDTM. [from Ross 1949 (p. 37)]. B: Tricolp(or)ate pollen grain of ± the same type as the grain in FRIES and Ross 1950, Fig. 7, p. 205 (Upper Cretaceous deposits, Åsen, Scania; slide made by Ross). — C, D: Pollen grains from Upper Cretaceous deposits, Åsen,

herewith, is synonymous with »intercolpium» (Fægri and Iversen 1950). The reasons for proposing the new term (and, supplementary, »apocolpia» for »polar areas») cannot, however, be dealt with here.]

The similarity between some of the pollen types in *Faramea* and some sporomorphs described under the generic name of *Tricolporites* does not imply that the plants producing the latter sporomorphs were related to Rubiaceae and the present day genus *Faramea*. In accordance with suggestions made in an earlier paper (Erdtman 1947) it seems, however, possible to speak of »*Tricolporites* (*Farameoidites*) *protrudens*» (instead of just *Tricolporites protrudens*). This would give megapalaeobotanists a hint of the possibility — whether great, slight, or non-existent, we do not know — of finding megascopical remains of *Faramea* or related plants in *Tricolporites protrudens*-bearing bed.

Palynological Laboratory, Bromma, March 1951.

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Scania (slides made by Ross). — E. *Faramea salicifolia* (Brazil; Krukoff 6207). a: equatorial view (250 ×). b: sclerine stratification (2000×). c: sculptine patterns at four adjustments of the microscope from high to low. d: aperture, equatorial view (about 2000 ×). — F. *Faramea amazonica* [Peru (Ucayali); Tessmann 3002)]. — G: *Faramea longicauda* (Ecuador; Steene 8024). — A—G: 1000 ×. — A.-L. Nilsson del.

Svensk Botanisk Tidskrift. Bd 45, H. 2. 1951.

ON THE POLLEN MORPHOLOGY OF BETULA NANA.

BY

J. TERASMÄE.

The pollen grains of *Betula nana* can be distinguished in most cases (if not always) from those of the Scandinavian tree birches by means of characters other than size. This has been realized by Dr. G. Erdtman during the last few years, but nobody has so far made a special study in order to settle the question definitely.

My first contacts with the problems of birch pollen occurred during a palynological investigation of Late Glacial beds on Gotland. These beds were particularly rich in birch pollen grains of different shapes and sizes and Dr. Erdtman suggested that I should at the same time study the *Betula nana* pollen question more thoroughly.

Given the possibility of distinguishing pollen grains of *Betula nana* from those of other Scandinavian birches it would be possible to compare, in greater detail than hitherto, the pollen diagrams from Northern Sweden (± rich in pollen grains of *Betula nana*) with those from Southern Sweden (less rich in or wholly destitute of dwarf birch pollen). It would, likewise, be possible to trace the entire Late Quaternary history of *Betula nana*, a complicated problem, still far from its solution. In a comprehensive review of the forest history of Central Europe, Firbas (1949) also discussed the *Betula nana* problem (especially during the Late Glacial period): »Blätter und Früchte von *Betula nana* gehören, wie man seit Nathorst weiss, zu den bezeichnendsten Resten der Glazialfloren. Sie wurden auch noch in einer so tiefen und heute so warm-trockenen Lage wie der innerböhmischen Elbniederung (Losert), weiter im Bereich der Lössböden des Unterreichsfelds (Steinberg) und ander-

wärts gefunden. Es ist daher sehr wahrscheinlich dass es sich dort, wo in waldloser Zeit *Betula* unter den Gehölzpollen vorherrscht, um *Betula nana* handelt (Firbas 1943 c). Es ist auch möglich, dass der spätglazialen Waldgrenze vielfach ein eigener *Betula nana*-reicher Gürtel vorgelagert war, ähnlich der heutigen »Unterzone der Zwergbirkentundra» im nördlichen Russland (Andrejew, nach Walter 1943). Er mag sich mit den vorrückenden Wäldern nach Norden verschoben haben, wie dies Bertsch vermutet und Faegri im südwestlichen Norwegen wahrscheinlich machen konnte. In solchen birkenreichen Proben können dann auch in waldlosen Gebieten bei der üblichen Art der Berechnung die NBP-Werte gering bleiben. Doch darf man deswegen nicht jeden Birkengipfel zu Beginn der spätglazialen Bewaldung als *Betula nana*-Gipfel bezeichnen. Die Pollenerzeugung der Zwergbirke ist offenbar gross. Nach Iversen (1942, 1947) ist der Pollen in rezenten Gyttjen grönländischer Seen gegenüber dem von Cyperaceen, Gramineen und Ericaceen erheblich übervertreten, wenn man die tatsächlichen Areale dieser Pflanzen mit den Pollenwerten vergleicht.»

It should be added that Hultén (1950) in his distributional atlas of Scandinavian vascular plants has published a detailed map of the present area of *Betula nana* in Scandinavia. Each dot in this and similar maps does not only represent a fact, a definite habitat of the species in question, it represents also a query: at what time and under what conditions did the plants spread to these habitats? In the case of *Betula nana* detailed pollen-analyses will no doubt be helpful in providing an answer to these questions.

The material used in this study (herbarium material and fresh pollen grains) was acetolyzed — and part of it chlorinated, too — in order to make a detailed investigation of sclerine stratification and sculptine details possible [methods, terms, and the way of drawing the illustrations (palynograms) are the same as those used at the Palynological Laboratory, Bromma].

The grains of *Betula nana* (Fig. 1: A and a; fresh material from Saxnäs, Lapland) are 3-porate, suboblate [about 21 × 25 μ; P/E . 100 = 86 (P: polar axis, E: maximum breadth of grain)]. Exine distinctly thinner (about 1.2 μ) than in the other birches. Mesoporial sexine as thick as nexine or slightly thicker. LO-pattern [faint, indistinct (L: lux; O: obscuritas; at high adjustment of the objective an LO-pattern exhibits small bright areas; at lower adjustment the same areas turn dark, separated by brighter channels)]. Arci ±

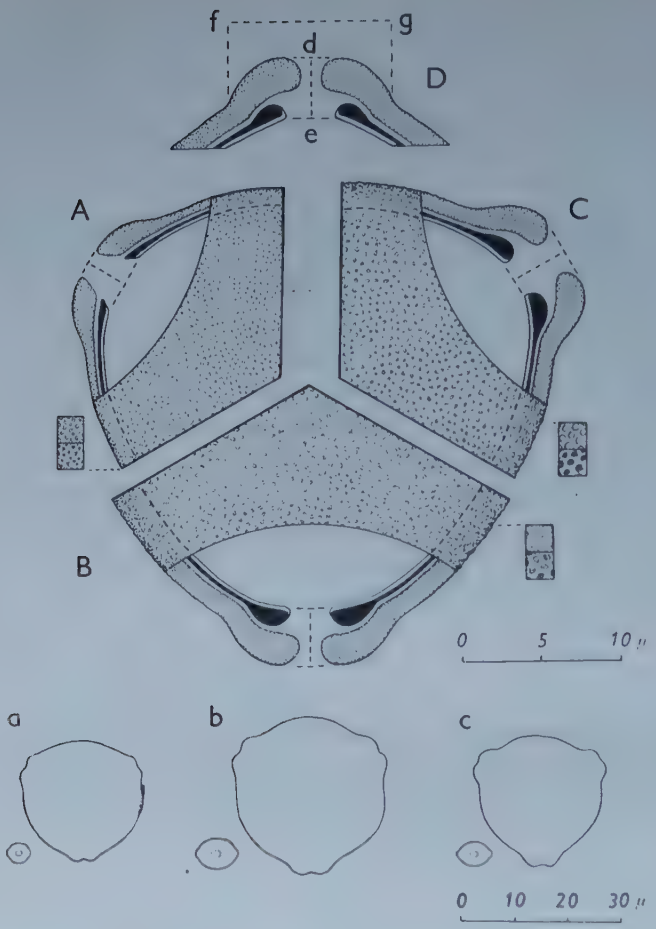

Fig. 1. Composite palynogram. A: *Betula nana* (2100×). B: *B. tortuosa* (2100×). C: *B. pubescens* (2100×). — a, b, c: »ambs» (= ambits; outlines of pollen grains viewed from one of the poles) of *B. nana*, *B. tortuosa*, and *B. pubescens* respectively [700×; the left hand details show the outline of the pollen grains in equatorial view (175×)]. D: equatorial cross-section through an aperture of a birch pollen grain. — A.-L. Nilsson del.

indistinct (more distinct in the tree birches). Apertures not so distinctly pouting as those in the other species (cf. Fig. 1 D; d–e in *B. nana* measures about 2.5 µ, in *B. pubescens* about 4.5 µ). Diameter of aperturiferous aspides (Fig. 1 D: f–g) shorter (about 7.5 µ) than in the other species (about 9.5 µ in *B. pubescens*). The grains in *B. pubescens* and *B. tortuosa* are more flattened (P/E . 100–77) than those in *B. nana*.

The pollen grains of *Betula pubescens* (Fig. 1 C and c) are 3-porate, suboblate (about 22 × 28 μ). Exine thickness about 1.6 μ (in *B. tortuosa* about 2 μ). Sexine about three times thicker than nexine. Ectosexine (tegillum) about three times thicker than endosexine. LO-pattern relatively distinct (cf. Fig. 1 C, right hand detail).

Further investigations are necessary in order to elucidate the possibilities — if any — of distinguishing between the pollen grains of different species of tree birches on a purely morphological basis. It should be noted, also, that the taxonomic status of *B. tortuosa* is still under debate.

Palynological Laboratory, Bromma, April 1951.

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Svensk Botanisk Tidskrift. Bd 45, H. 2. 1951.

NOTE SUR QUELQUES HÉPATIQUES RÉCOLTÉES PAR R. E. ET T. FRIES, EN 1922, AU MONT KÉNIA.

PAR

C. VANDEN BERGHEN.

Grâce à l'obligeance de Monsieur H. Persson, nous avons pu étudier quelques Hépatiques récoltées par R. et T. Fries, en 1922, au Mont Kénia (Afrique orientale anglaise), dans une région dont la flore hépaticologique est peu connue. La petite collection qui nous a été confiée et qui est conservée au Naturhistoriska Riksmuseum de Stockholm, présente un grand intérêt. Nous y avons reconnu deux espèces nouvelles pour la science: *Metzgeria convexa nov. sp.* et *Drepanolejeunea Friesii nov. sp.*

Metzgeria Raddi.

Metzgeria Elliotii Steph., Bull. Herb. Boiss., VII, p. 936 (1899); Vanden Berghen, Bull. Jard. Bot. Etat, Bruxelles, XIX, p. 195, fig. 18, E—I (1948).

Mont Kénia occid.; regio bambusina inferior in truncis Arundinariae alpinae, ca 2.500 m, janv. 1922, R. et T. Fries.

Metzgeria Elliotii Steph. nous était connu des hautes montagnes de l'est du Congo belge (Ruwenzori, Muhavura, Kahuzi). La plante y a été récoltée entre 2.400 et 4.150 m, principalement dans les bois de bambous. La découverte de cette espèce sur les flancs du Mont Kénia, également dans le *Bambusetum*, étend l'aire de dispersion connue de ce *Metzgeria*.

Metzgeria convexa Vanden Berghen *nov. sp.*

Dioica (?), corticola, ± gracilis e viridi pallens. Thallus 800—1000 μ latus, valde convexus, dichotomus. Costa utroque pagina corticalibus biseriatisque cellulis tecta. Alae margine singulis setulis ornatae. Alarum

cellulae 30—38 μ × 40—50 μ. Propagulae marginales, ovales, valde convexae. M. Elliotii Steph. valde affinis sed thallo valde convexo et forma propagularum differt.

Dioïque (?). Plante corticole formant des gazonnements vert-jaune. Thalle assez délicat, long de 1,5—2,5 cm, large de 800—1000 μ, *fortement convexe*; ramification régulièrement dichotomique, les portions du thalle comprises entre deux fourches successives étant longues de 2—3,5 mm; rameaux propagulifères étroits (220—300 μ) et souvent cucullés au sommet. Nervure large de 65—90 μ, nue ou pourvue de quelques poils ventraux courts, présentant, en coupe, 2 cellules corticales dorsales, ± 12 cellules internes, à membranes épaissies, disposées en 3 strates, et 2 cellules corticales ventrales. Ailes glabres dorsalement, rarement pourvues de quelques poils ventraux disséminés et isolés, à marge bordée de poils droits, habituellement isolés, longs de 170—280 μ. Cellules alaires assez régulièrement 5—6 gonales, à membranes minces parfois pourvues de petits trigones; dimensions des cellules médianes: 30—38 μ × 40—50 μ; cuticule lisse. Rameau ♀, réniforme lorsque étalé (400 μ × 550 μ), pourvu de ± 12 poils marginaux et ventraux longs de 90—180 μ. Reproduction végétative par des *propagules ovales, fortement convexes*, pourvus, de façon précoce, de poils marginaux droits, se développant à partir des cellules marginales de rameaux habituellement spécialisés et plus ou moins longuement atténués; dimensions des propagules: 85—120 μ × 100—160 μ (fig. 1).

Mont Kénia: regio alpina in truncis Vivis Philippiae hexagonae, ca 3.400 m, 2 fév. 1922, R. et T. Fries.

Metzgeria convexa Vanden Berghen *nov. sp.* est une plante propagulifère qui présente de fortes affinités avec *M. Elliotii* Steph. Elle s'en différencie, pourtant, par la convexité de son thalle et par l'aspect de ses propagules. Ceux-ci, en effet, sont fortement convexes et pourvus, précocement, de poils marginaux tandis que les propagules de *M. Elliotii* Steph. sont plans et ne possèdent pas de poils marginaux.

Anomalolejeunea (Spruce) Schiffn.

Anomalolejeunea pluriplicata (Pears.) Schiffn., Nat. Pflanzenfam., I, 3, p. 127 (1909); Steph., Sp. Hep., V, p. 297 (1913); Sim, Trans. Roy. Soc. South Afr., XV, p. 59, fig. (1926). — *Lejeunea* (*Anomalo-Lejeunea*) *pluriplicataa* Pears., Christiania Vid. Sels. For., I, p. 5, pl. II, fig. 1—19 (1887). — *Lejeunea* (*Strepsilejeunea*) *pluriplicata* Steph., Cat. Welwitsch's Afr. Plants, vol. II, 2, p. 319 (1901).

Mont Kénia occid.: regio bambusina inferior in truncis Arundinariae alpinae, ca 2.500 m, 28 janv. 1922, R. et T. Fries.

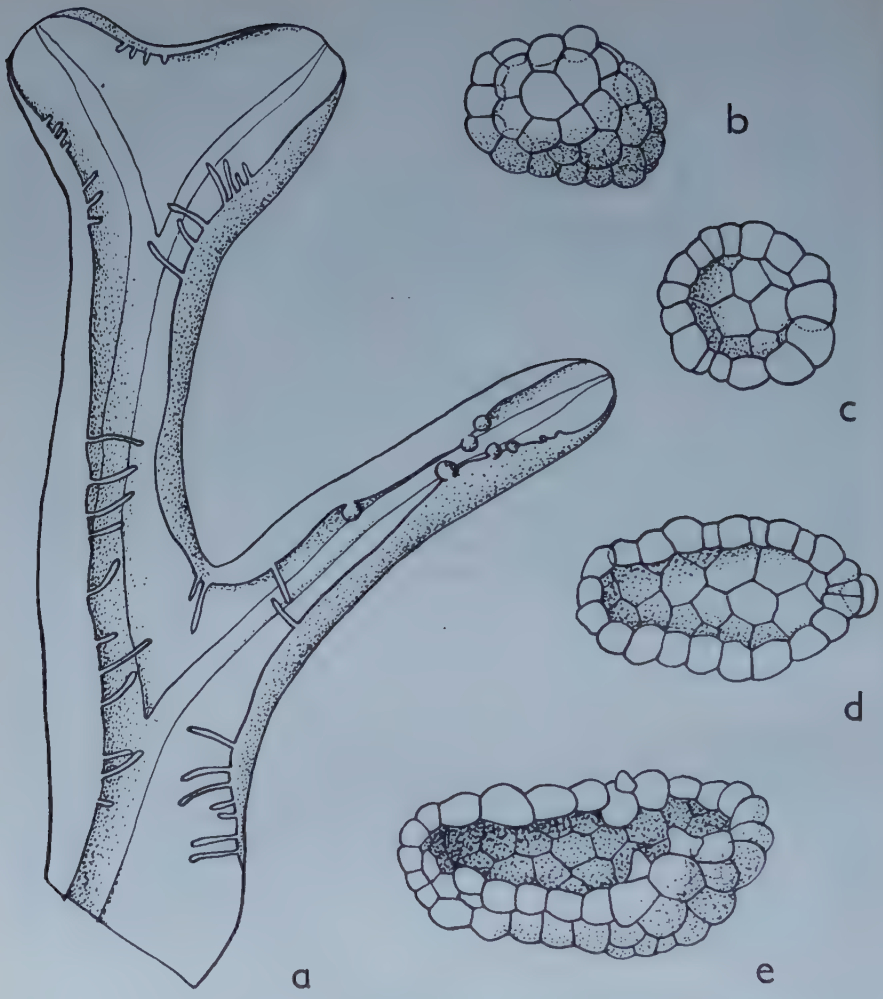

Fig. 1. *Metzgeria convexa* Vanden Berghen *nov. sp.* — a: vue ventrale du thalle (× 20); b, c, d et e: propagules (× 93) (Fries: type).

C'est avec un léger doute que nous rattachons la plante récoltée par Fries à l'espèce de Pearson. En effet, nous n'avons pas examiné l'échantillon type d'*Anomalolejeunea pluriplicata* (Pears.) Schiffn. et nous avons noté, chez la plante du Kénia (fig. 2), quelques caractères qui n'apparaissent pas dans la description et les figures de Pearson. C'est ainsi que les amphigastres caulinaires, au lieu d'être bilobés jusqu'au 1/4 ou au 1/3, sont simplement

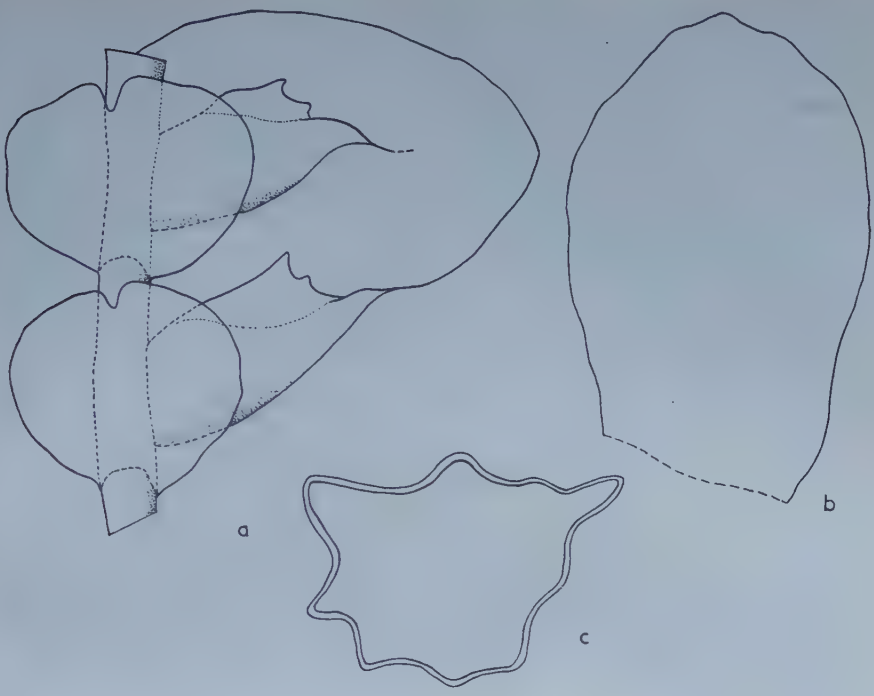

Fig. 2. *Anomalolejeunea pluriplicata* (Pears.) Schiffn. — a: vue ventrale d'un brin feuillé; b: bractéole ♀; c: coupe transversale dans le périanthe (× 93) (Fries).

émarginés. Le bord libre du lobule - en plus de la dent apicale - est pourvu d'une dent aiguë ou obtuse. Pearson décrit un lobule »unidentate» mais sa figure 4 représente très nettement les deux dents que nous avons observées. L'épi mâle est parfois formé de 6 paires de bractées et ne possède que 1—2 bractéoles vers sa base. La bractéole involucrale, »retuse or emarginate» pour Pearson, est plutôt tronquée ou, même, arrondie sur l'échantillon du Kénia. Ces différences, dans l'ignorance où nous sommes de l'amplitude des variations des caractères de l'espèce, ne nous ont pas paru suffisantes pour justifier la création d'une espèce nouvelle.

Anomalolejeunea pluriplicata (Pears.) Schiffn. a été récolté à Knysna et dans des autres régions forestières situées à l'est de Cap de Bonne Espérance. D'après Sim, *loc. cit.*, la plante y serait rare. *A. pluriplicata* (Pears.) Schiffn. a également été signalé dans l'Angola septentrional. La découverte de cette espèce sur le Mont Kénia est particulièrement intéressante.

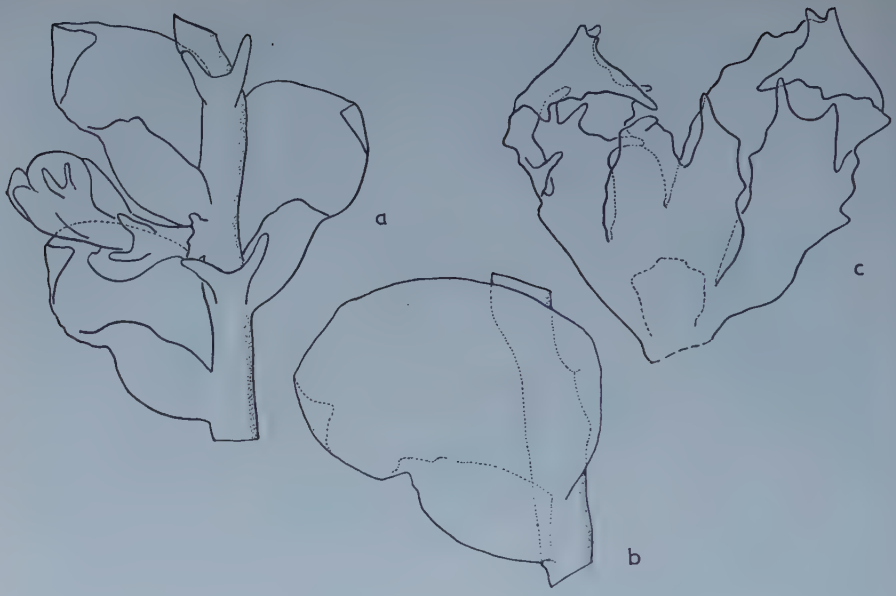

Fig. 3. *Drepanolejeunea Friesii* VANDEN BERGHEN *nov. sp.* — a: vue ventrale d'un brin feuillé; b: vue dorsale d'une feuille caulinaire; c: bractées et bractéole ♀ (× 93) (FRIES).

Drepanolejeunea (SPRUCE) SCHIFFN.

Drepanolejeunea Friesii VANDEN BERGHEN *nov. sp.*

Dioica (?). Pusilla, caule irregulariter pennata. Folia contigua vel leniter imbricata, lobo lanceolato, integro, concavo, acuto-acuminato incurvatoque, lobulo magno, inflato, elliptico, carena valde arcuata, margine integra, dente apicali obtuso. Cellulae foliorum subrectangulares, membranis trigonis parvis munitis et medio nodulosis; cellulae centrales: 14—18 μ × 16—22 μ; ocelli nulli. Amphigastria disco basi 4 cellulis lato et 2 lobis aciculatis 4—5 cellulis longis constituta. Inflorescentia ♀ in apice rami ± longi, una innovatione muniti. Bracteae erectae, lobo lanceolato, irregulariter dentato; lobulus ± rhombicus, irregulariter dentatus. Bracteola elliptica, irregulariter dentata, ad 1/3 bilobata, lobis acuto-acuminatis.

Dioïque (?). Plante délicate, corticole, formant des gazonnements vert-jaune. Tige irrégulièrement et densément pennée; diamètre: 50—65 μ. Feuilles contiguës ou très légèrement imbriquées, étalées-dressées, lobe débordant faiblement la tige, asymétrique, triangulaire-lancéolé, entier, concave, à sommet aigu-acuminé et incurvé, à bord dorsal fortement convexe, à bord ventral peu convexe ou droit, 190—230 μ × 300—320 μ; lobule relativement grand, enflé, elliptique, à carène fortement arquée formant un angle obtus avec le bord ventral du lobe, à bord libre entier, à dent apicale obtuse, ± 90 μ × 180 μ. Cellules foliaires à membranes

présentant de petits trigones à côtés concaves et des épaississements intermédiaires noduleux; cellules centrales et basilaires subrectangulaires: 14—18 μ × 16—22 μ; cellules marginales subcarrées: 10—12 μ × 12—14 μ; pas d'ocelles; cuticule lisse. Amphigastres à peine plus larges que la tige, formés d'un disque basilaire subrectangulaire formé de ± 6 cellules et de lobes aciculés, dressés ou divariqués, séparés par un sinus arrondi, longs de 4—5 cellules (1—2 séries de 2 cellules et 2—3 cellules mises bout à bout); dimensions: largeur des amphigastres: 90—120 μ, longueur des lobes: 45—60 μ. Inflorescence ♀ à l'extrémité d'un rameau plus ou moins allongé, présentant une innovation sous-florale. Bractées dressées, plus grandes que les feuilles végétatives, irrégulièrement dentées; lobe lancéolé à sommet longuement acuminé, 135 μ × 450 μ; lobule ± rhombique, 100 μ × 315 μ. Bractéole plus ou moins elliptique, bilobée jusqu'au tiers, à lobes aigus-acuminés, irrégulièrement dentée, 145 μ × 315 μ. Périanthe très juvénile (fig. 3).

Mont Kénia occid.: regio bambusina inferior in truncis Arundinariae alpinae, ca 2.500 m, 28 janv. 1922, R. et T. Fries.

Stephani (*Sp. Hep.*, V, p. 317, 1913), a recensé, pour l'Afrique, 11 espèces relevant du genre *Drepanolejeunea* (Spruce) Schiffn. Deux d'entre elles ont des lobes foliaires entiers: *D. clavicornis* Steph., *Hedwigia*, XXXV, p. 81, 1896, et *D. intorta* Besch. et Spruce, *Bull. Soc. Bot. Fr.*, XXXVI, 2, p. 188, 1889. Les descriptions de ces espèces ne peuvent s'appliquer à la plante du Kénia.

Drepanolejeunea Friesii Vanden Berghen *nov. sp.* doit être rattaché à la Section *Serrulatae* Herz., *Ann. bryol.*, III, p. 129, 1930.

Lejeunea Libert.

Lejeunea flava (Swartz) Nees, Naturg. Eur. Leb., III, p. 277 (1838).

Mont Kénia occid.; regio bambusina superior, ca 2.800 m, in truncis Arundinariae alpinae, fév. 1922, R. et T. Fries.
Id., ca 2.500 m, janv. 1922, R. et T. Fries.

Lejeunea flava (Swartz) Nees est une espèce subcosmopolite signalée en de nombreuses localités africaines, notamment, dans les montagnes de l'est du Congo belge.

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STUDIES ON THE ORIGIN OF THE ICELANDIC FLORA.

II. SAXIFRAGACEAE.

BY

ÁSKELL LÖVE and DORIS LÖVE.

I. Introduction.

From the point of view of gross geobotany studying the distribution of plants and their dispersal over the oceans, the Icelandic flora is of a considerable interest. This is the largest island on the submarine ridge crossing the Atlantic between Scotland and Greenland. It is surrounded by broad oceans, the shortest distances to other countries being about 300 km (to Greenland), about 420 km (to the Faeroes), about 800 km (to Scotland), and about 970 km (to Norway). According to geologists (cf. Thoroddsen, 1914), Iceland is built up mainly by basic eruptives from the Tertiary and Quaternary periods, subsequently moulded by abrasion, faults, and other denuding agencies. In Paleocene and Eocene about half the total thickness of the basalt was formed, and in Eocene lignite formation up to 50 meters thick was formed (cf. Kjartansson, 1940, 1943). Iceland became an isolated island already in the Tertiary, according to some geologists already in late Miocene (cf. Thoroddsen, l.c.), and although some geologists have suggested that its isolation might have been broken sometimes later, all the geological observations already made speak very strongly against that such a connection could have been formed after the beginning of the Quaternary period.

If the geologists are right in supposing that the isolation of Iceland has never been broken from pre-glacial times onward, it is not unlikely that this should have put marks on the flora met with in the country at present. As pointed out by Löve & Löve (1947),

not more than 30 per cent of the about 585 higher plants could have been introduced during historical times. All the remaining plants are suggested to have been met with in the country when it was first discovered by man about 1200 years ago. The great majority of these species must have invaded Iceland over some land connection as plant communities (cf, Chaney, 1925, 1936; Griggs, 1940; Hadač, 1948; Löve & Löve, 1947, 1949; Selander, 1950 a) in pre-glacial times — provided that the geologists are right as to the time of the unbroken isolation — but not more than 15 per cent of the present flora might, hypothetically, have been able to disperse from other countries in post-glacial and pre-historical times, most probably by aid of sea-currents only (cf. Löve & Löve, 1947).

More than half the number of species of the group which is suggested to have invaded Iceland over land only, show clearly gaps in their present distribution indicating survival of at least the last glaciation in unglaciated areas pointed out by geologists and biologists (cf. Lindroth, 1931; Gelting, 1934; Steere, 1937; Steindorsson, 1937, 1949; Thorarinsson, 1937; Löve & Löve, 1943, 1947; Löve, 1950, 1951 a, b). A rather great number of the species has, however, been able to disperse over wide areas in post-glacial times and fill completely the gaps, which must have existed in their distribution area when the glaciation was over.

The indigenous Icelandic flora might be classified into a number of groups according to their distribution outside Iceland and their possible route of dispersal towards the island. By aid of the excellent maps published by Hultén (1937, 1950), the flora might be classified into a number of equiformal progressive areas. As Iceland is, however, most frequently not near the centra of these areas, it might perhaps be more convenient to classify the flora into some fewer groups, indicating only their possible way, and perhaps time, of dispersal towards Iceland.

Due to the fact that many of the Icelandic plant species have not yet been thoroughly studied from the taxonomical viewpoints, the present writers have thought it to be most convenient to combine their studies on the origin of the Icelandic flora with cytotaxonomical investigations, especially as they are unable to make thorough genetical analyses due to lack of experimental facilities. The first paper in this series (Löve & Löve, 1947) included only the species *Cakile edentula* (Bigel.) Hook., which was found to belong to the small group of plants which might have dispersed

towards Iceland by aid of sea currents in post-glacial and prehistorical times. This supposition is further strengthened by later ecological investigations (LÖVE & LÖVE, unpubl.). The present paper, however, gives some informations about the sixteen species of Saxifragaceae known to occur in Iceland. *A priori*, only one of them has not been suggested to have survived the Glacial period in Iceland.

II. Cytotaxonomical part.

1. **Parnassia obtusiflora** RUPR.; LÖVE.

This species is the only Icelandic representative of the genus *Parnassia* (cf. LÖVE, 1950). It is identical with the tetraploid type of *P. palustris* L. s. lat. mentioned by ERLANDSSON (1942) from Sweden. The chromosome number 2 n = 36 has been determined in several individuals from different parts of Iceland, in the highland as well as lowland, belonging to the ssp. *tenuis* (WG.) LÖVE as well as ssp. *obtusiflora* (RUPR.) (= ssp. *typica* LÖVE).[1] This number has also been counted on material from northern Sweden (ERLANDSSON, l. c. LÖVE & LÖVE, 1944; LÖVE, 1950), northern Russia (ROZANOVA, 1940, 1946), and Labrador (LÖVE, 1950). The total distribution of the species is mapped by LÖVE (1950).

2. **Saxifraga Cotyledon** L.

Saxifraga Cotyledon is a species with a European, arctic-montane distribution (Fig. 1). In Iceland it is only met with in the south-

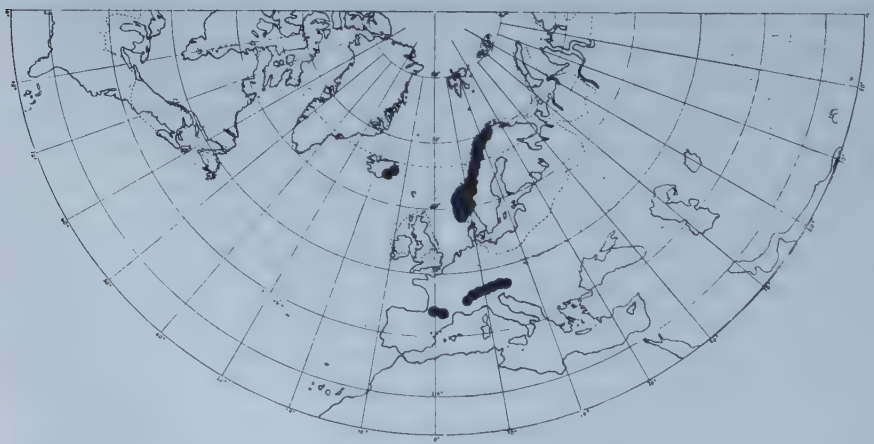

Fig. 1. The distribution area of *Saxifraga Cotyledon* L.

[1] As to this nomenclatural change, cf. SMITH, 1950.

Fig. 2. The Icelandic distribution of *Saxifraga Cotyledon* L.

eastern parts (Fig. 2), where it certainly has hibernated on icefree areas during at least the last glaciation. Its chromosome number in Iceland is 2 n = 28, as previously determined on European material by Skovsted (1934), Schoennagel (1931), and Mattick (in Tischler, 1950).

3. **Saxifraga Aizoon** Jacq.

Saxifraga Aizoon is met with in rather few localities in or in the neighbourhood of old nunatak-areas pointed out by geologists (cf. Thorarinsson, 1937) in eastern, northern, and western Iceland (Fig. 3).

The distribution of the species outside Iceland is apparently of the amphi-Atlantic type, as shown by Hultén (1950) and on the map in Fig. 4. As it is certainly of relict character in Europe it is suggested to have reached over there perhaps in early pre-glacial times. In Iceland it has certainly hibernated through the last glaciation close to its present localities, which all are within or in close neighbourhood of the icefree refuges. As its variation in

Fig. 3. The Icelandic distribution of *Saxifraga Aizoon* Jacq.

characters of edaphical and taxonomical value is very small so that only minor differences are detectable between material from the three isolated Icelandic centra of distribution, it might also be suggested that this lack of variation should be due to severe selection by previous glaciations. In the last interglacial the morphologically rather uniform Icelandic types might have been able to disperse all over the country, but during the last glaciation all but the populations of the few localities yet met with have been exterminated. The species also shows a rather weak power of dispersal if planted in garden soils in the lowland.

All Icelandic material of *S. Aizoon* is classifiable into the American-Greenlandic subspecies *neogaea* (Butt.) Löve & Löve (cf. Löve & Löve, 1948 b), the statement in the same paper showing also the ssp. *eu-Aizoon* Engl. & Irmsch. to occur in Iceland being a printing error only. In northern Norway a separate subspecies *Laestadii* Neum. is met with, but in southern Norway and other European areas the species is represented by ssp. *eu-Aizoon* (cf. Fig. 4).

The chromosome number has been counted in material from the cliffs of the mountain Brekkufjall in Borgarfjörður in the wes-

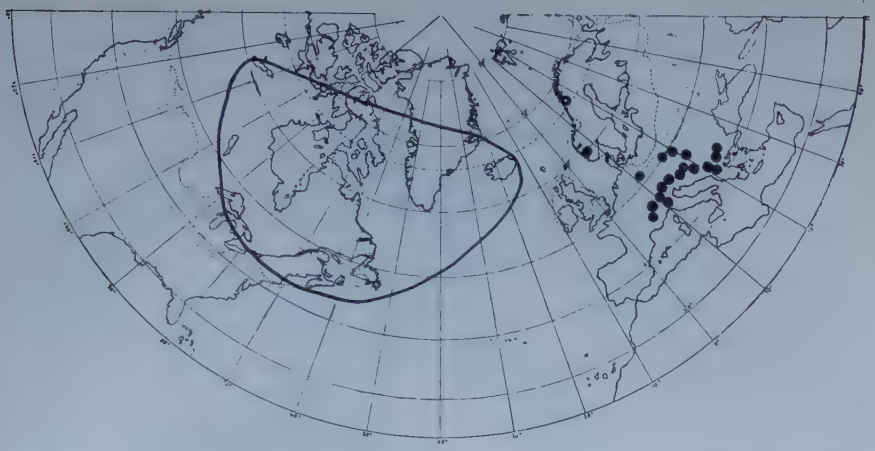

Fig. 4. The distribution area of *Saxifraga Aizoon* Jacq. Stretch line: ssp. *neogaea* (Butt.) Löve & Löve; dots: ssp. *eu-Aizoon* Engl. & Irmsch.; open ring: ssp. *Laestadii* Neum.

tern area of the species. It was found to be 2 n = 28 chromosomes. The same number has previously been counted by Skovsted (1934) and Mattick (in Tischler, 1950) on the ssp. *eu-Aizoon*.

4. **Saxifraga oppositifolia** L.

Taken in its widest sense, this collective species shows a circumpolar, arctic-montane distribution (cf. Hultén, 1950). According to Engler & Irmscher (1919), however, it is a »typus polymorphus» and its different phases are described on not less than 28 pages. Their taxonomical treatment of the species is, however, unsatisfactory from several points of view.

According to Andersson & Hesselmann (1900) the northern types of the species might easily be classified into the two forms, f. *reptans* And. & Hesselm. and f. *pulvinata* And. & Hesselm., the former one being loosely caespitose, with rather long, rooting branches and long internodes, the latter being cushion-like and having short internodes and shorter branches with nearly leafless flower-stalks, and densely packed leaves arranged in four rows. Both the forms are edaphically somewhat different (cf. Böcher, 1938 a; Gelting, 1934), and the f. *pulvinata* seems to have a more arctic (cf. Hultén, 1945) or high-montane distribution (cf. Selander, 1950 a, b). In Iceland only the f. *reptans* seems to be met with, in the highland as well as the lowland.

Fig. 5. The distribution area of *Saxifraga stellaris* L.

Although both these forms need closer studies, they are supposed to be of a great taxonomical value, not only due to their morphological, ecological, and geographical differences, but perhaps most due to their apparent differences in chromosome number making them biologically strongly isolated units. The main type of the species, or f. *reptans*, has been found to be diploid with 2 n = 26 chromosomes in Norway and Greenland (Skovsted, 1934; Böcher, 1941; Sörensen & Westergaard in Löve & Löve, 1948 b), as well as in all localities studied by the present writers in Iceland. The f. *pulvinata* is, however, found to be tetraploid with 2 n = 52 chromosomes in Spitzbergen (Flovik, 1940; cf. Hadač, 1944). If the tetraploid number is found to characterize the type in all parts of its distribution area, the arctic - high-montane type should certainly better be placed as a separate species, according to the principle enunciated by Nannfeldt (1938) and Löve (1951 c) for types differing in chromosome numbers as well as in morphological characters and geographical distribution. It seems also to have been named as the species *S. pulvinata* by Small (in Bull. N.Y. Bot. Gard. 2, 6, 1901, p. 172, cf. Hultén, 1945).

5. **Saxifraga stellaris** L.

This is a species of an amphi-Atlantic, arctic-montane distribution (Fig. 5). In Iceland it is a common plant, especially in wet localities, where it is found to show a considerable morphological variation.

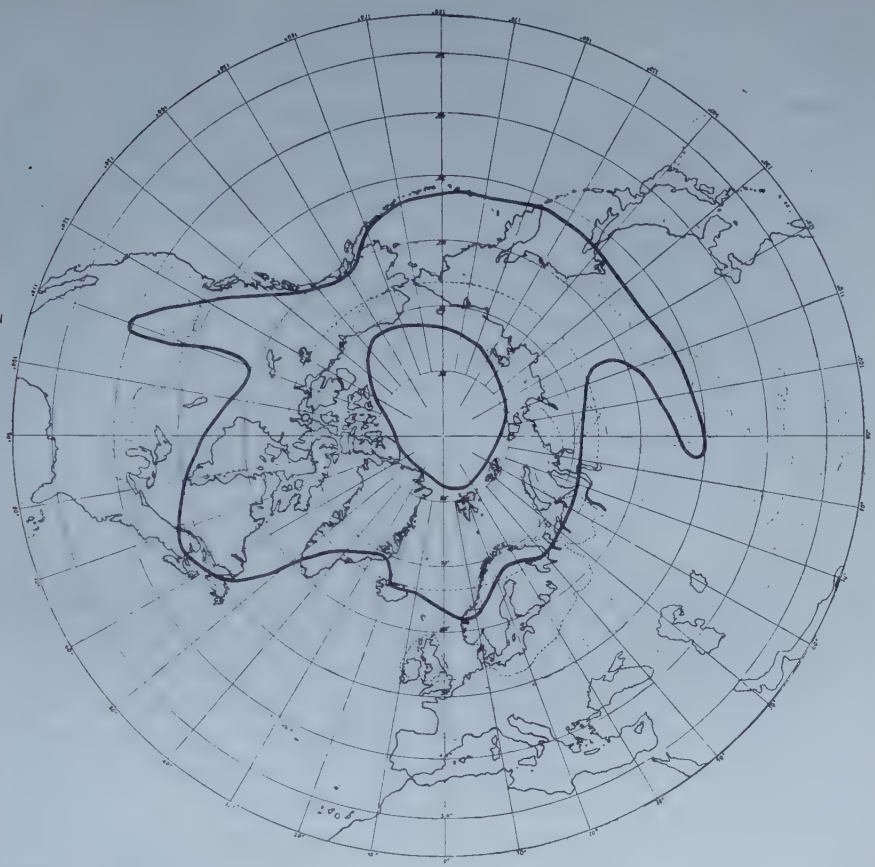

Fig. 6. The distribution area of *Saxifraga foliolosa* R. Br.

In spite of the wide variation met with all over the total distribution area of the species (cf. Böcher, 1938 a), only the chromosome number 2 n = 28 is met with in all localities yet studied in Iceland and other countries (Skovsted, 1934; Arwidsson, 1938; Böcher, 1938 b; Löve & Löve, 1948 b; Mattick in Tischler, 1950).

6. **Saxifraga foliolosa** R. Br.

This species, which is often erroneously placed as a variety of *S. stellaris* L. (cf. Mansfeld, 1940; Polunin, 1940; Fernald, 1950), is found to belong to the group of circumpolar, arctic-montane plants (Fig. 6). Although it is reported from some mountains of

Fig. 7. The Icelandic distribution of *Saxifraga foliolosa* R. Br.

Central Europe (cf. Hultén, 1950; Mansfeld, 1940), this might be based on some misunderstanding, as the Alpine plants are met with in the low-montane regions only, not in the high-montane regions as the arctic species (cf. Böcher, 1938 a; Hegi, 1906—1931, Vol. IV), and are morphologically somewhat different from the arctic material seen by the writers (cf. also Hylander in Gustafsson, 1947 a). Maybe the Alpine plants are only a viviparous variety of the species *S. stellaris* s. str., with the same number of chromosomes as that species.

The chromosome number of *S. foliolosa* has been found to be the octoploid number 2 n = 56 in material from Lappland (Arwidsson, 1938; Böcher, 1938 b; Löve & Löve, 1948 b), Spitzbergen (Flovik, 1940), and eastern Greenland (Sörensen & Westergaard in Löve & Löve, 1948 b). The somewhat deviating number 2 n = 64 seems to be met with in material from western Greenland (Harmsen, 1939). In Icelandic material from the more eastern locality of the only two ones yet known (Fig. 7; cf. Löve & Löve, 1948 a) the chromosome number was found to be 2 n = 56.

7. **Saxifraga nivalis** L.

According to Hultén (1950) this species shows a circumpolar, arctic-montane distribution. It is met with in some mountains in Great Britain and Ireland as well as in the Sudetes, but it seems to be absent from the Alps. In Iceland it is fairly common all over the country.

The chromosome number $2n = 28$ was reported for this species by Skovsted (1934), but this must be due to some error, as later investigations have clearly revealed that the chromosome number is $2n = 60$ (cf. Flovik, 1940; Sörensen & Westergaard in Löve & Löve, 1948 b; Böcher & Larsen, 1950). This number is also typical for all Icelandic material investigated.

8. **Saxifraga tenuis** (Wg.) H. Sm.

This is one of the two recognized species recently split out of the collective species *S. nivalis* L., the other one being *S. gaspensis* Fern. According to Smith (1920) and Polunin (1940) its distribution should be circumpolar, but although it is yet very incompletely known — perhaps mostly due to that too many taxonomists still include it only as a variety or form of *S. nivalis* (Gelting, 1934; Polunin, 1940; Hultén, 1950) — it is always found to be more high-arctic - montane than that species in its strict sense (cf. Böcher, 1938 a).

Even in Iceland is the distribution of *S. tenuis* incompletely known. It has certainly been collected from some localities in the high mountains of the central plateau as well as from the western and northern parts of the country, but it seems to be at least very rare in the southern parts of the island, where the snow-cover during winter is very thin or absent (cf. Löve, 1945; Stefansson & Steindorsson, 1948).

The chromosome number of Icelandic material of *S. tenuis* from Heiðarfjall at Öxnadalsheiði in the northern part of the country as well as from Brekkufjall in Borgarfjörður in its western part was found to be $2n = 20$, or the same number as previously determined on material from Scandinavia (Böcher, 1938 b; Löve & Löve, 1944), Spitzbergen (Flovik, 1940), and Greenland (Sörensen & Westergaard in Löve & Löve, 1948 b).

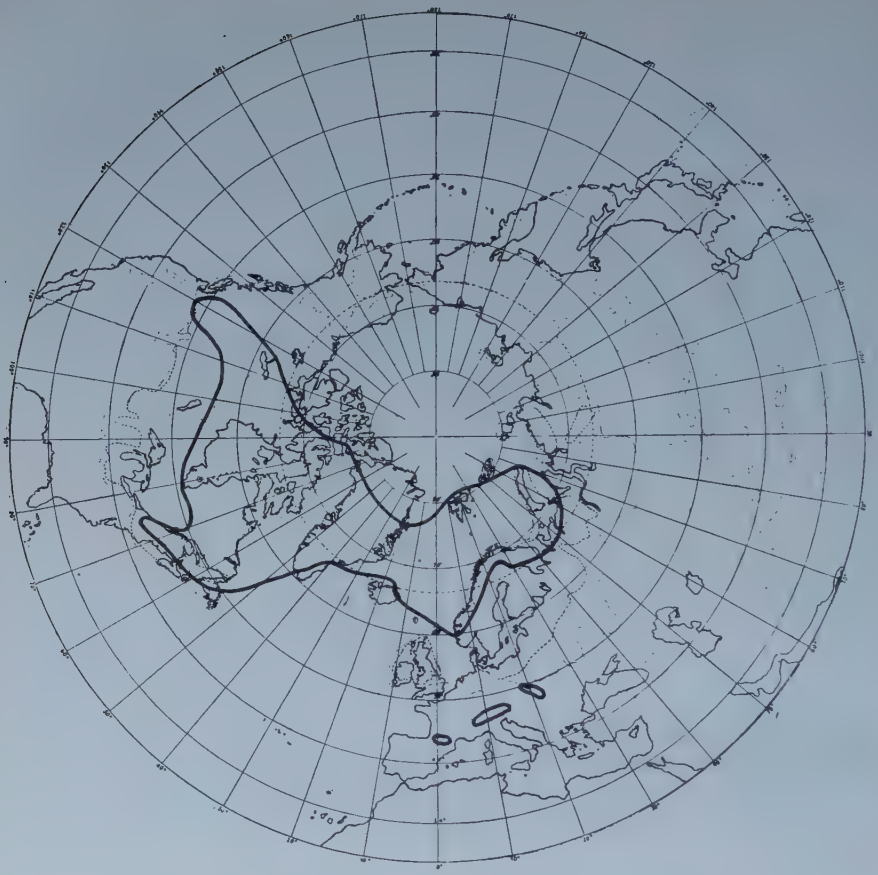

Fig. 8. The distribution area of *Saxifraga aizoides* L.

9. **Saxifraga aizoides** L.

The distribution of this species is rather like that of the species *S. Aizoon*, i.e. it belongs to the amphi-Atlantic group of arctic-montane species also met with in some mountains of central and southern Europe (Fig. 8).

Although Engler & Irmscher (1916) regard this species as a very polymorphous one, it is rather homogenous in Iceland, where it occurs only in the eastern parts (Fig. 9). Here it is often rather maritime although it is met with in some of the more continental inner parts of the country as well. As in Greenland (Böcher, 1938a), it certainly belongs to the group of glacial survivors in Iceland (Löve & Löve, 1947).

Fig. 9. The Icelandic distribution of *Saxifraga aizoides* L.

The chromosome number of Icelandic material was found to be 2 n = 26, or the same number as previously determined by Skovsted (1934), Böcher (1938 b; 1941), and Mattick (in Tischler, 1950).

10. **Saxifraga Hirculus** L.

Saxifraga Hirculus is a rather polymorphous species with a boreal-circumpolar distribution (cf. Hultén, 1950). Although not yet thoroughly investigated from the taxonomical points of view, it clearly includes some major geographical races, which should be named as distinct subspecies. The typical race, ssp. *Hirculus* (L.), or var. *typica* Hook., has more or less oblong petals, which are about three times as long as the sepals. It is met with in the southern parts of the distribution area of the species. Its chromosome number is 2 n = 32, as determined by the present writers on material from the neighbourhood of the town Kristianstad in the Swedish province of Scania. The arctic-montane race, var. *alpina* Engl. & Irmsch., or ssp. *propinqua* (R. Br.) Löve & Löve, subsp. nov. (*S. propinqua* Brown, 1821; cf. Simmons, 1906), is loosely tufted

and has obovate petals which are about twice as long as the sepals. It seems to be the only major race met with in Iceland, where it, however, also includes the variety *ochroleuca* Om. (cf. Omang, 1937) with oval-oboval petals, which are light yellow without darker stains. The chromosome number of this latter subspecies has been counted on material from different parts of Iceland and was found to be 2 n = 32. The same number has been determined by Flovik (1940) on the same subspecies, and most possibly the material found to have that number in Greenland (Sörensen & Westergaard in Löve & Löve, 1948 b) has belonged to that subspecies, too. The number 2 n = 28 given for the species *S. Hirculus* by Sokolovskaja & Strelkova (1938) from Pamir and Altai is supposed to be an inexact count for 2 n = 32.

11. **Saxifraga granulata** L.

This species is a recent introduction to Iceland, although it grows very well in the single locality yet known (cf. Fridriksson, 1934; Gröntved, 1942). In Europe the chromosome numbers 2 n = 32, 46—60, 48, 52, 56—60, and more than 60 have been determined by several cytologists (cf. Löve & Löve, 1948 b; Tischler, 1950). The Icelandic material has been found to have 2 n = c. 52 chromosomes.

12. **Saxifraga cernua** L.

This species seems almost never to fructify in Iceland, where it is common in wet localities in the mountains, except for the southern and southwestern parts of the country. It belongs to the circumpolar arctic-montane plants met with in the mountains of Central Europe as well as all over northern Siberia (cf. Hultén, 1950).

The chromosome number of the species seems to be somewhat variable, as the numbers yet published are 2 n = 50 (Chiarugi in Tischler, 1950), 2 n = 60 (Sörensen & Westergaard in Löve & Löve, 1948 b), and 2 n = c. 66 (Skovsted, 1934). Perhaps the variation is only due to difficulties in counting exactly the many and crowded chromosomes. In the Icelandic material the number 2 n = 64 or almost exactly 64 was determined in plants from some localities in the north.

13. **Saxifraga rivularis** L.

Saxifraga rivularis is a considerably variable species, which if taken in its wider sense has a circumpolar, arctic-montane distribution, lacks in the mountains of Central Europe but has a continuous distribution in northern Siberia (cf. Hultén, 1950). In Iceland it is common in all mountainous regions.

The species is clearly a collective one, as shown by the fact that two different chromosome numbers have been found to occur within its boundaries, *viz.* the diploid number $2n = 26$ chromosomes counted by Flovik (1940) on material from Spitzbergen, and the tetraploid number $2n = 52$ (Sörensen & Westergaard in Löve & Löve, 1948 b), or $2n = 56$ (Böcher, 1938 b) from Greenland. The material from northern Iceland studied by the present writers was found to have $2n = 52$ chromosomes. The collective species needs a close taxonomical revision connected to cytological and geographical studies (cf. Löve, 1951 c).

14. **Saxifraga caespitosa** L.

As pointed out by Webb (1948, 1950 a, b) it seems to be most convenient not to treat this species in the very collective sense as done by Engler & Irmscher (1916, 1919). In stead of that the type treated by them as ssp. *decipiens* (Ehrh.) Engl. & Irmsch. should be regarded as a separate species, but the two types described by Linnaeus (1753) as *S. caespitosa* L. and *S. groenlandica* L. are to be brought together under the first name.

According to Hultén (1950) the species *S. groenlandica* belongs to his distribution group 8, which includes circumpolar arctic-montane plants occurring in the mountains of Central Europe and with continuous distribution in northern Siberia. This is true for the species in its wider sense, including also the ssp. *decipiens* mentioned above. The species *S. caespitosa* in its strict sense, however, is not met with in Central Europe, but should certainly belong to Hultén's group 6, which includes circumpolar, arctic-montane plants lacking in the mountains of Central Europe but with continuous distribution in northern Siberia. The species is rather common in the montane areas of Scandinavia. It is met with in two localities in Scotland and one locality in Wales, but

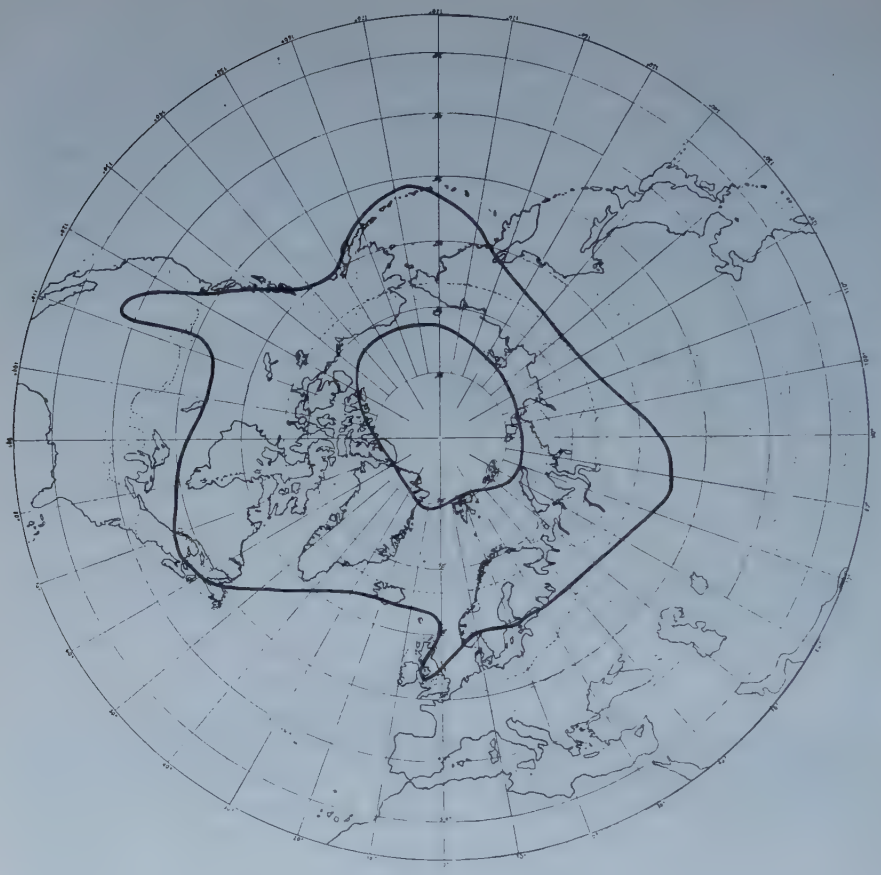

Fig. 10. The distribution area of *Saxifraga caespitosa* L.

is absent from Ireland and the Faeroes (cf. Webb, 1950 a, b). In Iceland it is extremely rare in the south, and it seems to be absent from the lowlands except for the northernmost parts. In the mountains of northern Iceland where it is covered by snow during the winter months it seems to be fairly frequent. Its total distribution is shown approximatively on the map in Fig. 10.

The chromosome number of *S. caespitosa* has been determined by Flovik (1940), who counted $2n = 80$ chromosomes in material from Spitzbergen, and by Böcher (1938 b) and Harmsen (in Löve & Löve, 1948 b), who counted the numbers $2n = c.\ 84$ and 80, respectively, on material from Greenland. The former number might have been an inexact count for $2n = 80$, as later

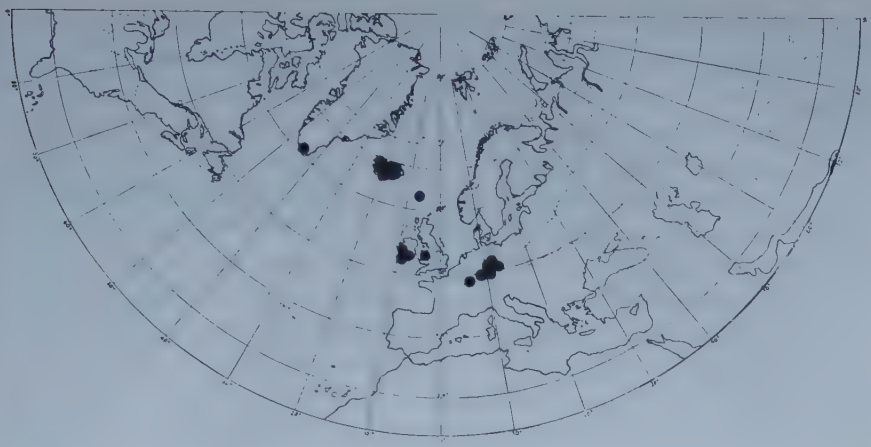

Fig. 11. The distribution area of *Saxifraga rosacea* MOENCH.

counted by BÖCHER & LARSEN (1950) on Greenlandic material. Material from northern Iceland has been found to be decaploid with $2n = 80$ chromosomes.

15. **Saxifraga rosacea** MOENCH.

This species is identical with the ssp. *decipiens* (EHRH.) ENGL. & IRMSCH. of *S. caespitosa* s. lat. As mentioned above, this type should, according to the morphological and geographical investigations performed by WEBB (1948, 1950 a, b), be regarded as a distinct species, but as the name *S. decipiens* EHRH. used by RASMUSSEN (1936), LÖVE (1945), and several others was published only as a *nomen nudum*, the species has to be named *S. rosacea* MOENCH (cf. WEBB, l.c.).

The species *S. rosacea* is found in some small area in Central Europe, perhaps in one locality on the Snowdon range in Wales, and in southern and western Ireland (WEBB, 1950 a, b). It seems to be rather rare on the Faeroes, but in Iceland it is met with in the lowland in all parts of the country and is fairly frequent up to at least 500—600 m. s. m. in South-Iceland. In Greenland it is reported only from between the south coastland and the Holsteinsborg region, according to ENGLER & IRMSCHER (1916) and BÖCHER (1938 a). Its total distribution area is shown in Fig. 11.

Only rather inexact chromosome counts have as yet been published on material classified as *S. rosacea*, but as the species has been confused with some related species in Europe, some of the

numbers might not have been counted on this species in its strict sense. TISCHLER (1950) refers to papers reporting the numbers 2 n = 32, 56—65, and c. 64, but WEBB (1950 a, b) gives the two tentative counts 2 n = c. 48 and 64 from Ireland. As the chromosomes are small and crowded, it might often be difficult to obtain an exact count, and in fact the two numbers 2 n = 32 (WHYTE, 1930) and 2 n = c. 64 (PHILP, 1934) were determined on the same material or at least on material from the same small area, Clare Island in Ireland. If the two numbers 48 and 64, however, are really typical for the Irish material, this clearly indicates that the species has to be still closer investigated from the taxonomical point of view (cf. LÖVE, 1951 c).

The present writers have studied material from southern as well as northern Iceland, fixed in chrome-acetic-formaline and stained with crystal violet. In all the plants they were able to ascertain that the chromosome number was exactly 2 n = 64 or at least c. 64, i.e. the octoploid number.

16. **Saxifraga hypnoides** L.

ENGLER & IRMSCHER (1919) recognized two subspecies within this species, i.e. ssp. *boreali-atlantica* of the northern and maritime Europe, and the ssp. *continentalis* of central and southern France and northern Spain. WEBB (1948, 1950 a, b) has, however, clearly demonstrated that these two types should better be treated as two distinct species, *S. hypnoides* L. sens. orig. and *S. continentalis* (ENGL. & IRMSCH.) WEBB. Taken in that sense, the species *S. hypnoides* belongs to the group of European, Atlantic plants numbered as group 19 by HULTÉN (1950), but not to his group 12. It is restricted to Great Britain and Ireland, some spot in western Norway, the Faeroes. Iceland, and the Vosges, near Gerardmer (cf. WEBB, 1950 a, b). Its total distribution is shown in Fig. 12.

According to HULTÉN (1950), *S. hypnoides* belongs to the very few species of Scandinavia which have only an isolated western area, grouped by him in the migrational group X. He regards the 22 species of this group as being not hardy plants which have certainly reached their northern positions after the Glacial period. This might be true for most of these species. In view of the fact, however, that *S. hypnoides* is a common plant from near the sea-level up to at least 1600 meters in the mountains in Iceland, mainly

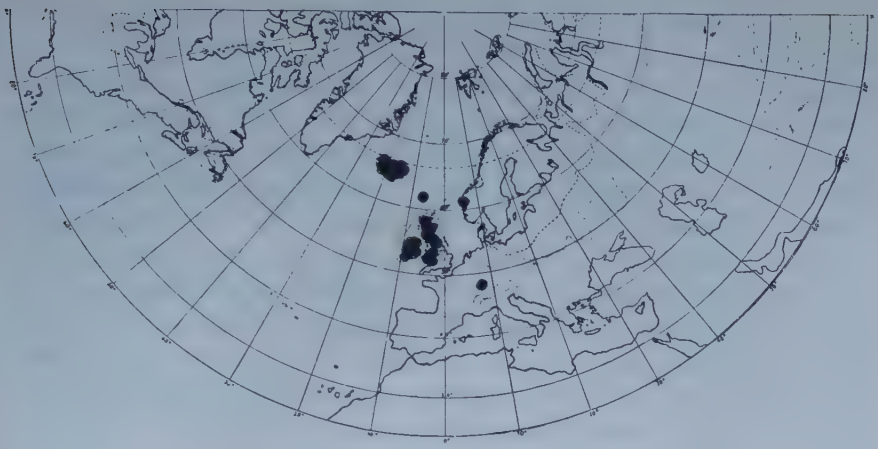

Fig. 12. The distribution area of *Saxifraga hypnoides* L.

on cliffs and rocky slopes but very frequently at the rivers and rills, that species certainly cannot be regarded but as hardy. In Iceland and the Faeroes it seems to belong to the certain hibernators of at least the last glaciation, and it might be suggested that it should also have survived the last glaciation in neighbourhood of its present localities in western Norway. As at least five, if not seven, of the plants classified by HULTÉN (l.c.) in this migrational group are common in the Faeroes not only in the lowland, it might be suggested that these species are from the last interglacial there and, perhaps, in western Norway as well.

The chromosome number of *Saxifraga hypnoides* s. lat. has been determined by SKOVSTED (1934), who counted 2 n = 44 and 58 in two cultivated individuals from unknown sources. WEBB (1950 a, b) gives the two tentative numbers 2 n = c. 48 and 64 from Ireland. The present writers have made exact determinations on material from the highland between Eyjafjörður and Skagafjörður in northern Iceland and at Þingvellir in southern Iceland, as well as from the lowlands in Skagafjörður, Borgarfjörður and Mosfellssveit. All the individuals were found to be characterized by exactly the same number, or 2 n = 48 chromosomes. Therefore, the species is only found to be hexaploid in Iceland. Due to that two different numbers seem to be met with in the Irish material of the species *sensu* WEBB (l.c.), it is highly desirable that its cytological behaviour in all parts of its distribution area should be further investigated in connection to still closer taxonomical analysis of the material.

III. Discussion.

Although all but one of the sixteen Icelandic representatives of the family Saxifragaceae certainly belong to the group of glacial survivors in Iceland, they have certainly not reached the country the same way or at the same time, as shown by their distribution outside Iceland. The long time of isolation from other populations of the same major geographical races as they are found to belong to themselves seems, however, not to have been able to create morphological differences making them at least weak endemics. In fact, already known endemics are not very few within the Icelandic flora, in view of the high frequency of species which have at least survived the last glaciation in the country. The total indigenous flora of higher plants is found to include more than 30 per cent of endemics, but if the not yet thoroughly studied representatives of the apomictic genera *Hieracium* (cf. Omang, 1938, and in Löve, 1945) and *Taraxacum* (cf. Christiansen, 1942; Haglund in Löve, 1945) are excluded, still about 4 per cent of known endemics remains. The already known Icelandic endemics outside *Hieracium* and *Taraxacum* are the following ones: *Ophioglossum vulgatum* L. var. *islandicum* Löve & Löve; *Glyceria fluitans* (L.) R. Br. var. *islandica* Löve; *Sesleria varia* (Jacq.) Wettst. ssp. *islandica* Löve; *Roegneria Doniana* (White) Meld. var. *Stefanssonii* Meld.; *Roegneria borealis* (Turcz.) Nevski var. *islandica* Meld.; *Dactylorchis maculata* (L.) Vermln. ssp. *islandica* Löve & Löve; *Silene maritima* With. ssp. *islandica* Löve & Löve; *Papaver radicatum* Rottb. ssp. *islandicum* Löve; *Papaver radicatum* Rottb. ssp. *Stefanssonii* Löve; *Anthyllis Vulneraria* L. ssp. *borealis* Rouy; *Euphrasia rotundifolia* Pugsl.; *Euphrasia Davidssonii* Pugsl., and *Galium pumilum* Murr. ssp. *islandicum* Sterner (cf. Gröntved, 1942; Jalas, 1950; Löve, 1945, 1950, 1951 a, b; Löve & Löve, 1948 b; Melderis, 1950; Pugsley, 1933; Sterner, 1944). Some forms, which are not yet thoroughly studied, might also belong to this group, among them *Saxifraga Hirculus* L. ssp. *propinqua* (R. Br.) Löve & Löve var. *ochroleuca* Om., some *Euphrasiae*, *Alchemillae*, and *Papaver*types. To it might also belong the near-endemics also met with in the Faeroes, i.e. *Papaver radicatum* Rottb. ssp. *faeroeënse* Lundstr. and *Alchemilla faeroeënse* (Lge) Bus.; the former one might have been formed by natural selection during some part of the Glacial period, most probably in some isolated areas in eastern

Iceland or between Iceland and the Faeroes, while the latter one is an alloploid species which most probably has been formed after hybridization between the usually apomictic *Alchemilla alpina* L. and *A. vestita* (Bus.) Raunk. (Löve & Löve, unpubl.). It is also suggested to have been formed in some isolated locality in eastern Iceland during some part of the Glacial period. All hypotheses on its being a closer relative to now isolated species of the Pyrenées and the Alps (references by Gustafsson, 1947) must be based on some mistakes as well as lacking knowledge on species formation through alloploidy. That such alloploid species may be formed several times in different localities is well known (cf. Clausen, Keck & Hiesey, 1945; Ownbey, 1950).

The Icelandic representatives of Saxifragaceae belong mainly to the group of circumpolar boreal or arctic plants, classified by Hultén (1950) into three different subgroups numbered by him as No. 1, 6, and 8. Perhaps between 30 and 40 per cent of the indigenous Icelandic flora should be classified into this distribution group. Most of the species of it are not met with in the British Isles, making it most probable that they might have dispersed to the island in early glacial or perhaps pre-glacial time from Greenland or over a hypothetical land connection uniting Scandinavia, Iceland, Greenland and North America. Those of them found in the British Isles and the Faeroes might, of course, also have reached Iceland the southern way, perhaps somewhat later than the other ones. Among the Icelandic Saxifragaceae of this group *Parnassia obtusiflora*, *Saxifraga tenuis*, and *S. foliolosa* are not found in the British Isles, while *S. oppositifolia*, *S. nivalis*, *S. Hirculus*, *S. cernua*, *S. rivularis*, and *S. caespitosa* are met with in some British mountains. Being absent in the Faeroes it is, however, unlikely that *S. cernua*, *S. Hirculus*, and *S. caespitosa* have dispersed to Iceland over an ancient land connection via the Faeroes and Scotland, especially as the Icelandic and British populations of at least *S. Hirculus* seem not to belong to the same geographical race. That this is not completely excluded, however, is indicated by the fact that the western European *Sesleria varia* (Jacq.) Wettst. is met with in Iceland although it is not yet detected in the Faeroes.

Three of the Icelandic species of Saxifragaceae, i.e. *S. Cotyledon*, *S. hypnoides*, and *S. rosacea*, seem to belong to the group of European plants classified by Hultén (1950) into the groups No. 4 and 19. To the former group, or the European, arctic-montane

plants, only *S. Cotyledon* belongs, which group includes only three other Icelandic species, or the *Hieracium* group *Nigrescentia* Elfstr., *Myosotis silvatica* Ehrh. ssp. *frigida* T. Vest., and *Epilobium alsinifolium* Vill. The total distribution of these plants might be suggested to indicate a rather high age of the species in question. In Iceland they show a rather small morphological variation, and only fourteen microspecies of the *Hieracium* group *Nigrescentia* have as yet been detected in the country. To the latter group, or the European, Atlantic plants, belong the other two species mentioned, although *S. rosacea* seems to have dispersed as far as to southernmost Greenland. This group seems also to be represented in Iceland by *Luzula congesta* (Thuill.) Lej., *Sagina subulata* (Sw.) C. Presl., *Callitriche pedunculata* DC., *Thymus Drucei* Ronn.; Jalas, *Sesleria varia* (Jacq.) Wettst., and perhaps *Dactylorchis Fuchsii* (Druce) Vermln. Certainly, this group has dispersed via a land connection over Scotland and the Faeroes, where it is represented by at least eighteen species. Although this dispersal might have taken place relatively late, the Icelandic representatives of both the subgroups have certainly reached the island not later than in the last interglacial, as all the Icelandic representatives show a present distribution area clearly indicating a survival in the country during at least the last glaciation.

The three species of Icelandic Saxifragaceae left, i.e. *S. stellaris*, *S. aizoides*, and *S. Aizoon*, all belong to the amphi-Atlantic plants, or the group 11 of Hultén (1950). The first one is frequent all over the country, and although variable it seems not to differ morphologically from Greenlandic or Scandinavian material. The second one is met with in the eastern parts of the country only, where it is fairly frequent. Also in this species morphological variations typical for the Icelandic populations only have as yet not been observed. The third species is a very rare plant in Iceland, met with in few places only, from where it seems to have great difficulties in dispersing to other places. Morphologically, all the Icelandic populations clearly belong to the American subspecies *neogaea*, which, thus, must have been formed before the species dispersed eastwards or westwards to or from Iceland. In Norway, however, the northernmost locality is characterized by a ssp. *Laestadii*, which is ecologically as well as morphologically distinct from all other types of the species, while the more southern Norwegian populations are classified as ssp. *eu-Aizoon* only. It remains

as yet an open question whether other European populations are also morphologically and ecologically differentiated. They are all yet classified as ssp. *eu-Aizoon* only.

It also remains an open question whether HULTÉN (1937, 1950) is right in suggesting that the amphi-Atlantic distribution types should be remnants of a circumpolar distribution only. All species reaching Iceland and not able to disperse by aid of sea-currents must without exception have reached the country through some land connection (cf. LÖVE & LÖVE, 1947). Although these plants might, hypothetically, have dispersed towards east and west from Beringia in ancient times and later on disappeared except in their present amphi-Atlantic area, their occurrence in Iceland indicates a land connection to the area in America and/or Scandinavia. Perhaps more easily the present distribution of this group of plants might be assumed to be the remnants only of an original center at a Tertiary land connection in the northern Atlantic, which might have disappeared in late Miocene or at least before the beginning of the Quaternary glaciations (cf. THORODDSEN, 1914). Whether this land connection is to be explained by the assumption of a trans-Atlantic bridge, the Scandic landmass, or by the hypothesis of continental drift (cf. BAKER, 1932; CAIN, 1944; DE GEER, 1912; HADAČ, 1948; LINDROTH, 1931; DU TOIT, 1937, 1938; THORODDSEN, 1914; WEGMANN, 1948), remains an open question beyond the scope of the present discussion. From such a hypothetical Atlantic center of origin a very typical equiformal progressive area of distribution in all directions might be formed, including arctic-boreal types only met with in Iceland and the Faeroes up to species distributed all the way east to Ural and west of Hudson Bay. It is very unlikely from the combined cytogenetical and plant geographical point of view that all boreal and arctic species have originated in one or two centra only.

As to the time of the great dispersal of plants and animals among the land masses of the northern hemisphere, most biogeographers have supposed that they have taken place as late as in Quaternary times (cf. HULTÉN, 1937; GELTING, 1941). Large Quaternary movements or displacements, however, do not meet with the approval of geologists (cf. WEGMANN, 1948). As evolution seems to be considerably slower than previously supposed (cf. SMALL, 1949, CHANEY, 1936), especially in the regions in question (cf. SUESSENGUTH, 1950; STERNER, 1943), the opinion might be advocated that all

the species with distribution areas from the smallest amphi-Atlantic ones up to the circumpolar ones should be regarded as Tertiary types which have changed only minimally during the Quaternary period. This last suggestion seems also to be strongly supported by the relatively small and unimportant variation in arctic high-polyploids as, e.g., the octoploid *Acetosella graminifolia* (LAMB.) LÖVE, which is at present met with in widely separated regions split out of a circumpolar arctic area indicating a high age (cf. LÖVE, 1943; FERNALD, 1950). From the biogeographical and evolutionary points of view it is, therefore, not to be regarded as impossible that the great dispersal might have taken place even in middle or late Tertiary, at the time when the Scandic landmass or other direct connection of the continents existed in the northern Atlantic and Polar Sea (cf. DE GEER, 1912; WEGMANN, 1948).

The amphi-Atlantic species *Saxifraga aizoides* and *S. Aizoon* ought, perhaps, more correctly be classified into a group of American, arctic-montane plants, as they are distributed in America from its northeastern corner to southern Alberta and Saskatchewan, respectively (cf. FERNALD, 1950). Some of the groups classified by HULTÉN (1950) as arctic-montane or arctic plants with large gaps in Siberia ought perhaps as well be classified into a group of American, arctic-montane plants reaching Europe through the hypothetical, pre-glacial land connection, or even as the remnants of the still more hypothetical Atlantic or Scandic center mentioned above. Both suggestions might be supported by the fact that although many of the plants occurring in Iceland and found to have a wide distribution in America have reached Scandinavia or even northern Russia, some species belonging to the same distribution groups inside America have only reached Iceland or Greenland. Known examples of Icelandic plants of this group not reaching Scandinavia or other parts of Europe are: *Zostera stenophylla* RAF., *Elymus mollis* TRIN., *Platanthera hyperborea* (L.) LINDL., *Salix cordifolia* PURSH ssp. *callicarpaea* (TRAUTV.) LÖVE, *Cakile edentula* (BIGEL.) HOOK., *Galium Brandegei* A. GRAY, and perhaps even *Chamaenerion latifolium* (L.) SWEET, *Carex Lyngbyei* HORN., *Leucorchis straminea* (FERN.) LÖVE [two the last of which are also met with in the Faeroes], *Saxifraga Aizoon* JACQ. ssp. *neogaea* (BUTT.) LÖVE & LÖVE [although other races of it are found in Europe], *Plantago juncoides* LAM. var. *glauca* (HORN.) FERN. [which, according to DEVOLD & SCHOLANDER, 1933, is not

identical with the Scandinavian *P. maritima* L. var. *borealis* (Lge)], and *Roegneria Doniana* (White)Meld. [although it is also met with in one or two localities in Scotland]. Of these species, *Zostera*, *Cakile*, and *Plantago* might, hypothetically, have dispersed over the Atlantic Ocean by aid of sea-currents in post-glacial times (cf. Löve & Löve, 1947), while all the other species are certainly only able to disperse over land or narrow sounds. Few examples of species which might belong to this group but have reached Europe via the Icelandic connection are the plants of the group 2 by Hultén (1950), i.e. *Carex holostoma* Drej., *Gentianella detonsa* (Rottb.) G. Don, *Pedicularis flammea* L., *Primula stricta* Horn., *Cerastium arcticum* Lge, *Rhinanthus groenlandicus* Chab., *Rhinanthus borealis* (Sterneck)Marshall (cf. Selander, 1950 a), *Arenaria humifusa* Wg., and *Potentilla pulchella* R. Br., although the two last-named species have at least not yet been detected in Iceland. Also the species *Carex adelostoma* V. Krecz. is suggested to belong to this group, although it might perhaps more correctly be placed with the amphi-Atlantic plants of Hultén's group 10. It is placed by Hultén (1950) in his group 48, including plants with insufficiently known total areas, though with the remark that it might be an endemic with outposts to northern Ural. It is recently detected in Iceland (Davidsson, 1947; Stefansson & Steindorsson, 1948; Löve & Löve, 1948 b), as well as in Labrador (Raymond, 1950 a, b). The species of Hultén's group 7 might also belong to this American group reaching Scandinavia via the north-Atlantic connection, *viz. Stellaria calycantha* (Led.)Bong., *Epilobium lactiflorum* Hausskn., *Carex nardina* Fr., *Campanula uniflora* L., *Erigeron unalaschense* (DC.) Vierh., *Epilobium Hornemannii* Rchb., as well as *Rhododendron lapponicum* (L.)Wg. and *Draba crassifolia* Grah., although the two last-mentioned ones are not yet found in Iceland.

The plants classified above as the American element in the Icelandic flora have certainly dispersed to the island prior to at least the last glaciation. Their present distribution inside Iceland clearly reveals their being glacial survivors, exactly as they are found to be within the Scandinavian flora (cf. Selander, 1950 a). The hypothesis of their dispersal in pre-glacial or perhaps middle or early Tertiary times cannot, however, be emphasized on the basis of their present distribution areas. The high age of this element might, however, be shown by the fact that the primitive moss spe-

cies *Bryoxiphium norvegicum* (Brid.) Mitten. belongs to the American element in the Icelandic flora. In all places where it is met with it seems to be an early pre-glacial relic (cf. Steere, 1937). Much more indicative for the high age of at least some of the Icelandic flora elements is, however, the fact demonstrated by Lindquist (1947) that in Tertiary — perhaps Eocene, but not later than Miocene — the species *Betula callosa* Notö was met with in Þrimilsdalur in Iceland. That species grows in some Icelandic forests even at present (Löve, 1945; Lindquist, 1945, 1947). All observations made seem to support the view that this arctic-montane tree has been a continuous member of the Icelandic flora since in early Tertiary, and it is very unlikely that it should be the only old member of the flora of higher plants surviving all the Glacial period in Iceland. In fact, especially forest plant communities are found to be extremely stable and include the same species groups for millions of years, as very clearly demonstrated by Chaney (1925, 1936) studying the American redwood forests from Oligocene to our times. It is certainly not a mere coincidence that the Icelandic forests at present include practically exactly the same plant communities and almost all the same plant species as the montane birch forests of Scandinavia (Löve, 1951 b).

Although the hypothesis set forth by Hultén (1937, 1950), understanding most or all the areas with smaller or greater gaps somewhere in America or Asia as reductions only of an earlier complete circumpolar area of distribution, has been justly criticized (cf. Nannfeldt, 1940; Samuelsson, 1943; Selander, 1950a), his theory of equiformal progressive areas of distribution is certainly agreed upon by all present geobotanists. That theory is certainly one of the most stimulating and plausible attempts ever made in order to get full understanding of the dispersal of plants from their locality of origin to their present distribution areas. It is necessary, however, to point out and stress vigorously the weakness of the hypothesis of dispersal of plants over the present continents only, especially as the flora of isolated islands clearly indicates that some land connections must have disappeared after their dispersal had been completed. The present writers are fully convinced that the great majority of arctic and boreal plants must have dispersed over land only (cf. Griggs, 1940; Hadač, 1948; Löve & Löve, 1947, 1949). They find it, however, very improbable that the present distribution area of species now met with exclu-

sively in eastern North America, Iceland, and northwestern Europe should be the remnants only of a previously complete circumpolar area, produced by dispersal from Beringia in both directions (cf. MARIE-VICTORIN, 1938; NANNFELDT, 1940, 1947; SAMUELSSON, 1943; SELANDER, 1950 a). The variation met with between the American-Greenlandic-Icelandic and the European subspecies of *Saxifraga Aizoon* might, however, perhaps be taken as an indication of the correctness of HULTÉN's hypothesis, at least for some species. The Icelandic populations are certainly glacial survivors, as are the European populations, but when the Icelandic plants are found to be indistinguishable from the American material, the European populations are clearly distinct subspecies. As demonstrated by SMALL in several interesting papers (cf. SMALL, 1949), the stability of species and subspecies might often reach over considerably longer space of time than necessary for the assumptions made by HULTÉN (l.c.).

Better than mere meditations as to the age and evolution of the flora elements are, however, biological and experimental comparisons of material from several of the isolated areas. As shown in the present paper, none of the species of Saxifragaceae found in Iceland have evolved by aid of alterations in their number of chromosomes after their arrival in Iceland, and their visible morphological and ecological variations are not found to separate them from foreign material. They might, however, have gained some different variations in their invisible characters of value for their edaphic reactions, although this will not be revealed without thorough experimental analysis. Such an experimental analysis including morphologically similar as well as different material from different populations of widely separated areas might give excellent and rather reliable informations as to the variation of characters of evolutionary value within as well as between races isolated for a longer or shorter period. Even cytogenetical analysis of such material should certainly be of great value for the understanding of the evolution and dispersal of the biota of the northern hemisphere. Maybe such investigations of plants like the Icelandic representatives of Saxifragaceae could give reliable informations as to the real affinities of the floras at both sides of the Atlantic. They might at least reveal if the types met with at the eastern coast of America and the western coast of Europe are closer related than types from the most eastern and western populations on both the

continental sides of the amphi-Atlantic areas. Although an intricate problem, no attempts have as yet been made in order to get certain informations on the cytogenetical relationship of distant populations of the same species isolated through oceans for a long time. Such investigations are, however, suggested to be one of the most reliable methods known for getting reliable informations about the origin of the floras of both the sides of the Atlantic. If made on representative material, such studies might, perhaps, give excellent indications also on the geological history of the northern Atlantic as well as on the speed of evolution in higher plants.

Summary.

(1) Iceland is the largest island of the northern Atlantic, isolated by oceans perhaps all the time from late Miocene or at least from before the beginning of the last glaciation and during all post-glacial times. Its flora is poor in species number, including only about 585 higher plants. Of these, not more than 30 per cent have been introduced in historical times, not more than 15 per cent might have dispersed by aid of, mainly, sea-currents in post-glacial and pre-historical times, while the rest is supposed to have dispersed towards the island as plant communities over land.

(2) Cytological data are given for Icelandic material of sixteen species of Saxifragaceae. The following species and numbers were studied: *Parnassia obtusiflora*, 2 n = 36; *Saxifraga Cotyledon*, 2 n = 28; *S. Aizoon*, 2 n = 28; *S. oppositifolia*, 2 n = 26; *S. stellaris*, 2 n = 28; *S. foliolosa*, 2 n = 56; *S. nivalis*, 2 n = 60; *S. tenuis*, 2 n = 20; *S. aizoides*, 2 n = 26; *S. Hirculus*, 2 n = 32; *S. granulata*, 2 n = c. 52; *S. cernua*, 2 n = 64; *S. rivularis*, 2 n = 52; *S. caespitosa*, 2 n = 80; *S. rosacea*, 2 n = 64; and *S. hypnoides*, 2 n = 48.

(3) Informations on the distribution of all the species are given in the text and/or in maps of their Icelandic or total areas known.

(4) All the species are found to be morphologically indistinguishable from foreign material, except perhaps one less known type of *S. Hirculus*. The Icelandic material of *S. Hirculus* belongs to the arctic-montane ssp. *propinqua*, while that of *S. Aizoon* is found to be identical with the American ssp. *neogaea*.

(5) It is pointed out that more than 30 per cent of endemics are met with in the Icelandic flora, but if the apomictic genera *Taraxa-*

cum and *Hieracium* are excluded, still about 4 per cent of known endemics remains. These endemics are listed.

(6) All but one of the Icelandic representatives of Saxifragaceae are found to belong to the group of glacial survivors.

(7) Eight of the species of the family belong to the group of circumpolar boreal or arctic plants. That group includes between 30 and 40 per cent of the indigenous flora elements.

(8) Three Icelandic *Saxifragae* belong to the groups of European Atlantic and arctic-montane plants. These groups are represented in Iceland by a few other species only.

(9) Three Icelandic species of *Saxifraga* belong to the group of amphi-Atlantic plants. The origin and history of this type of distribution in discussed. In that connection the American element in the Icelandic flora is listed.

(10) The occurrence of the moss *Bryoxiphium norvegicum* in Iceland is regarded as a strong support to the hypothesis of the pre-glacial age of the flora. Its high age is further supported by that the species *Betula callosa* seems to have been continuously met with in Iceland from early Tertiary times onwards.

(11) Although the writers join issue with HULTÉN (1937, 1950) as to the origin of the amphi-Atlantic distribution areas, his ideas might be found to be supported by the differences met with between American-Icelandic and European material of *Saxifraga Aizoon*.

(12) It is suggested that intense cytogenetical investigations on the relationship of populations from both the sides of the Atlantic, at the coasts as well as inland, might give reliable informations as to the origin of these floras, their ways of dispersal and evolution. Such studies might also give some indirect informations on the geological age and history of the northern Atlantic.

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BIDRAG TILL JÄMTLANDS KÄRLVÄXTFLORA.

AV

BENGT DANIELSSON.

Den följande artförteckningen grundar sig huvudsakligen på anteckningar från exkursioner gjorda under åren 1946—1950. Urvalet har gjorts med ledning av Langes provinsflora (1938) och Hulténs atlas (1950). Här nedan ha sålunda i allmänhet endast medtagits sådana lokaler, som ej äro upptagna i dessa verk.

Jag har att tacka assistent Teuvo Äyräpää för att han ställt lokaluppgifter till mitt förfogande, samt prof. J. A. Nannfeldt och dr E. Asplund för hjälp med bestämning av mitt pressade material.

Lokalangivelserna grunda sig på generalstabskartan samt i fråga om fjällsocknarna på Svenska fjällkartan blad 7 och 8. Lokalerna i Föllinge ligga samtliga inom 8 km radie från kyrkan. Nomenklaturen är i stort sett i enlighet med Hultén (op. cit.).

Flera av mina lokaler äro från Hårkans stränder i Föllinge sn. En reglering av detta vattendrag är planerad, och därvid komma dessa lokaler att i stor utsträckning sättas under vatten. Stränderna upptagas till betydande del av kalkkärr med stor artrikedom. Särskilt anmärkningsvärda äro kärren med *Orchis cruenta*, *O. Traunsteineri* och *O. maculata* med talrika övergångsformer. En intressant lokal för *Salix reticulata* kommer likaledes att dränkas. Vidare kommer säkerligen den märkliga *Ledum*-lokalen (Stenar 1950) att påverkas, även om den inte direkt blir översvämmad. En grundlig botanisk undersökning av de berörda områdena är enligt min mening synnerligen angelägen, innan regleringsplanerna om något år förverkligas.

De intressantaste fynden torde vara de för Frostviken nya *Carex elongata*, *C. Hostiana* och *Oxytropis lapponica* samt *Salix reticulata* i Föllinge.

Artförteckning:

Actaea spicata. — Frostviken: bäckravin på Jormliklumpens SV-sida.

Agropyron caninum. — Föllinge: i granskog på platån N om Nyland. Ingår här i praktfull högörtvegetation med bl. a. *Aconitum septentrionale*, *Mulgedium alpinum*, *Actaea spicata*, *Poa remota* och *Milium effusum*.

A. latiglume. — Frostviken: Klumpliklumpen på serpentin, Raudek. Confirm. E. Asplund.

Arabis hirsuta. — Frostviken: ex. från Raudek visa en väsentligt glesare hårbeklädnad än låglandsformen och torde sålunda kunna föras till var. *subalpestris* Ahlfvengr. (jfr Selander 1950 II p. 13).

Asplenium septentrionale. — Berg: Hoverberget.

A. viride. — Frostviken: Gellvernokko i S- och O-branterna, Grukksfjället, Klumpliklumpen på serpentin.

Bartsia alpina. — Offerdal: flerst. vid Åkerån.

Blechnum spicant. — Frostviken: Tvärliklumpens O- och S-sidor mkt rikl., fjällen S om Storfjället NO Vågens tullstation (T. Äyräpää).

Botrychium boreale. — Frostviken: Grukksfjället i rasbrant å N-toppen.

Cardamine flexuosa var. *ambigua.* — Frostviken: vid leden Jormlien—Raudek.

Carex adelostoma. — Frostviken: Frostviken: vid en tjärn i reg. alp. SO om riksröset 197 A. Confirm. E. Asplund.

C. appropinquata. — Föllinge: strax SV Ockern i kärret med *Orchis*-arterna (jfr nedan).

C. elongata. — Frostviken: Vallåns utlopp i ett dike NV landsvägsbron. Confirm. E. Asplund. Arten är ny för Frostviken och tidigare blott en gång anträffad i Jämtlands fjällområde, nämligen i Åre sn mellan Enafors och Handöl (Smith 1920). Lokalen är Sveriges nordligaste, men både i Finland och Norge ligga utbredningsgränserna väsentligt längre norrut (jfr Hultén 1950). Man får i Hulténs atlas ett intryck av att arten är stadd i spridning och att förekomsten i Frostviken utgör en förpostlokal. Växtplatsen på kulturskapad ståndort tyder även på detta (dock finnes ju även den möjligheten, att lokalen är tillkommen genom spridning från någon ännu oupptäckt lokal i närheten). - Beläggexemplar ha överlämnats till Riksmuseum.

C. globularis. — Föllinge: V om Sandvikssjön, Lisjömyren.

C. heleonastes. — Föllinge: nära Björnpussbodarna vid en liten tjärn. - Confirm. E. Asplund.

C. Hostiana. — Frostviken: vid p. 647 ONO Vågens tullstation i nedre reg. subalp. Lokalen meddelad av assistent T. Äyräpää. Confirm. E. Asplund. — Arten är ny för Frostviken, och lokalen ligger c:a 14 mil N om den enligt Hultén (op. cit.) nordligaste svenska. I Riksmusei samlingar ligger emellertid ett ark *C. Hostiana* insamlat ytterligare 2 mil längre norrut, vid Ankarede lappkapell av K. O. E. Stenström. Bestämningen är bekräftad av Alvar Palmgren. Fyndet synes inte vara publicerat tidigare. *Carex Hostiana* förekommer även vid Storlien

och har av allt att döma västerifrån invandrat till Jämtland. Passagen över Skanderna tycks ha gått över de låga passen vid Storlien och Gäddede (jfr HULTÉN op. cit. karta 403).

På lokalen vid Vågens tullstation förekommer även rikligt av en hybrid med *Carex Hostiana*. Den andra konstituenten är enligt E. ASPLUND vansklig att fastställa. Man kan dock gissa på *C. flava*, som förekommer rikligt på samma lokal. Hybriden liknar mycket den på Skurdalshöjden vid Storlien förekommande *C. Hostiana*-bastarden (jfr LANGE op. cit. p. 63). — Beläggexemplar av *C. Hostiana* och dess hybrid ha av upptäckaren överlämnats till Riksmuseet.

C. livida. — Föllinge: vid en tjärn SV om bron över Hårkan. Hammerdal: Sörvattnet vid Gisselås.

C. pauciflora. — Frostviken: antecknad från fem lokaler i området riksröset 197-Raudek-berget vid Sätern nära Jormlien.

Cerastium glabratum HARTM. — Frostviken: Klumpliklumpen på serpentin. Confirm. E. ASPLUND. Arten växer här tillsammans med *Cerastium alpinum* L. s. str., vilket mera sällan förekommer (jfr t.ex. ARWIDSSON 1943 p. 197). Mellanformer uppträda också mellan de båda arterna.

Chenopodium album. — Frostviken: vid Konsum i Jormvattnet.

Chrysanthemum Leucanthemum. — Frostviken: utefter hela landsvägen Bågede-Jormlien.

Convallaria majalis. — Hotagen: Höberg.

Corallorhiza trifida. — Frostviken: myr Ö Raudek, nära Selkentjahkstugan.

Cryptogramma crispa. — Hotagen: Munsfjällets topp år 1919. Meddelad av notarie E. LIDMAN.

Cypripedium calceolus. — Föllinge: på många ställen i närheten av kyrkbyn t. ex. björkkärr Ö Näsaforsen ett 70-tal blommande individ år 1949; vid Ockerns V strand spars., Forsåsen rikl.

Cystopteris montana. — Frostviken: Grukksfjället. Föllinge: strax SV om Ockern, vid Andåns nedre lopp, S om bron över Hårkan.

Dactylis glomerata. — Hammerdal: vid vägkant i byn.

Draba norvegica. — Frostviken: Grukksfjället, Gellvernokko, fjället S Siliesjaure, Vallåns raviner. Samtliga lokaler: det. E. ASPLUND.

Drosera rotundifolia. — Frostviken: myr Ö Raudek reg. subalp. Betydligt sällsyntare V om Jorm än *Drosera anglica*.

Dryas octopetala. — Frostviken: Grukksfjället är till största delen täckt av *Dryas*-hed. Norr därom synas emellertid vidsträcktare fjällsippsheder vara en sällsynthet i Frostviken. På Raurotjuolta förekommer dock en mindre hed i toppområdet (jfr DANIELSSON 1948). På Gellvernokko förekommer på ostsidan rasbrantsartad *Dryas*-hed, medan på jämnare mark fältskiktet domineras av icke kalkkrävande arter. I stora områden på Gellvernokko och i dess omgivningar är emellertid den kalkrika berggrunden täckt med oligotrofa glacifluviala bildningar. — På serpentinfjället Klumpliklumpen observerades några *Dryas*-kuddar vid toppröset. På Klumpliklumpen kunde man f. ö. vänta sig att finna *Arenaria norvegica*, som är näranog konstant på serpentin i Åsele lappmark (RUNE 1947). Trots att jag speciellt letade efter *Arenaria*, kunde den dock inte anträffas här. Troligt är dock, att *Arenaria norvegica* har flera,

ännu oupptäckta lokaler på Frostvikens talrika serpentinförekomster (jfr karta hos T. Du Rietz 1935).

Epilobium alsinifolium × *palustre.* — Frostviken: Jormliklumpens SV-sluttning. Det. E. Asplund.

E. montanum. — Hotagen: Höberg.

Epipogium aphyllum. — Hammerdal: vid en bäck nära Ötjärn. Ett 10-tal individ aug. 1946.

Fragaria vesca. — Frostviken: Tvärliklumpens S-brant.

Galeopsis bifida. — Frostviken: Tvärliklumpen, en sydbrant NV Klumpliklumpen. Hotagen: Höberg.

Gymnadenia conopsea. — Frostviken: Klumpliklumpen, Selkentjahk, Raudek, Storlidfjället, vid riksröset 197. Föllinge: f. *fl. alb.* spars. bland huvudformen invid Näsaforsens kraftstation.

Hypericum maculatum. — Hammerdal: vid Fyrån nära sågen.

Isoëtes lacustris. — Hotagen: Kingen vid båtlänningen nära Höberg. Det. E. Asplund.

Juncus castaneus. — Frostviken: V om Raurotjuolta vid bron över Gaustjokk, Grukksfjället.

Kobresia simpliciuscula. — Frostviken: Raudek rikl. vid en bäckravin å fjällets S del. Confirm. E. Asplund. Arten växer i en brant *Dryas-Carex rupestris*-hed med sydlig exposition. Strax ovanför lokalen finnas hällar med bl. a. *Sedum villosum* och *Saxifraga Cotyledon.* Enligt vad dr Lange haft vänligheten meddela mig i brev har arten tidigare anträffats på Raudek av apotekare C. M. Norrman; lokalen är också registrerad i Hulténs atlas. Om denna lokal är den av Norrman upptäckta är mig dock obekant. Beläggex. ha överlämnats till Riksmuseet. — Lokalen är landets näst nordligaste, endast den nyupptäckta växtplatsen i Lycksele lappmark är nordligare (Rune 1949). Dessa lokaler ha ungefär samma karaktär. Jfr fig. 1 och fig. hos Rune (op. cit.)

Leucorchis albida. — Frostviken: Grukksfjället rikl., Gellvernokko flerst. i rasbranterna, leden Raudek-Jormlien reg. silv., fjället med riksröset 197 A, fjället S Siliesjaure.

Listera cordata. — Frostviken: Grukksfjället i övre reg. subalp., Leipikmon, fjället med riksröset 197 A i reg. alp. Hotagen: vid Höberg nära båtlänningen.

L. ovata. — Föllinge: kärr strax SV Ockern.

Lobelia Dortmanna. — Hotagen: Kingen vid båtlänningen nära Höberg. Uppgiven från denna sjö redan av P. Olsson (1884).

Lotus corniculatus. — Frostviken: Grukksfjället rikl. i rasmark, Klumpliklumpen.

Matteuccia Struthiopteris. — Föllinge: i granskog strax NV Ockern.

Matricaria discoidea. — Frostviken: Jormlien vid vägkanten. Ny för Frostviken.

Nigritella nigra. — Utöver uppgifterna hos Stenar (1946—47) kan här tilläggas Föllinge: på ängar mellan apoteket och sjön 15—20 ex. 1949. Lokalen anvisad av herr R. Eliasson, Föllinge.

Nymphaea alba ssp. *candida.* — Föllinge: i en tjärn strax SV om bron över Hårkan.

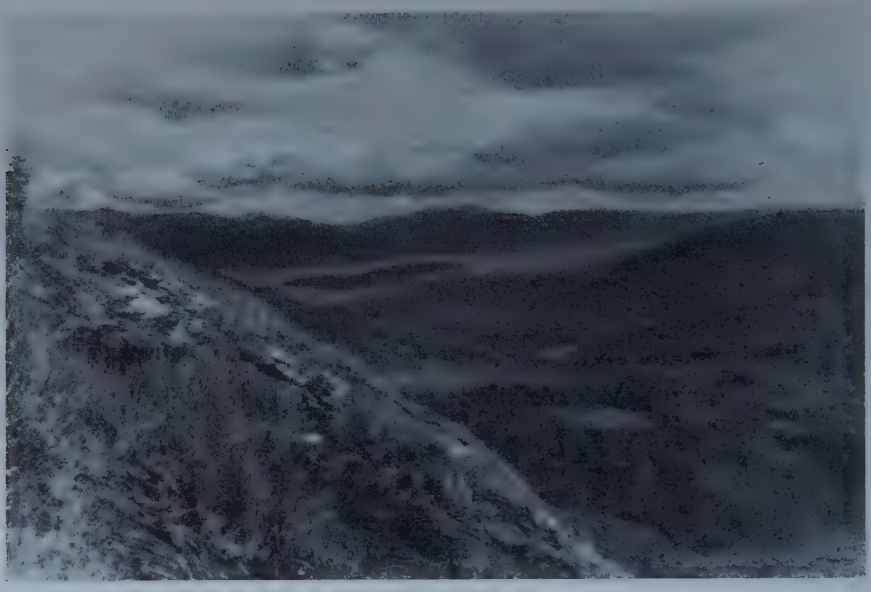

Fig. 1. Från *Kobresia*-lokalen på Raudek. I bakgrunden syns bl. a. Klumpliklumpen och L. Jormsjön. På platån nedom fjället vida *Scirpus caespitosus*-myrar, i vars kanter *Narthecium ossifragum* förekommer. Foto: förf. 14/8 1950.

Orchis cruenta. — Hammerdal: tjärn V om sågen vid Fyrån. Föllinge: kärr strax SV Ockern. Det. J. A. Nannfeldt.

O. incarnata. — Hammerdal: tjärn V om sågen vid Fyrån. Det. J. A. Nannfeldt.

O. maculata. — Ex. från Frostviken: reg. silv. å Grukksfjället nära Rörsjön utmärkas av ljusgröna, ofläckade blad av spadlik form samt ha läppens mittflik långt utdragen. Samma typ iakttogs på Jormliklumpen, här liksom å Grukksfjället i högörtvegetation. Exemplaren likna habituellt bilden av *O. Fuchsii* Druce hos Nordhagen (1948 p. 138) med undantag av att axet på mina ex. är kortare. Enl. vad prof. Nannfeldt meddelat mig i brev kunna emellertid mina exemplar inte beläggas med detta namn.

O. Traunsteineri. — Hammerdal: vid en tjärn V om sågen vid Fyrån. Föllinge: kärr vid Hårkan SV Ockern. Båda lokalerna: det. J. A. Nannfeldt. Exemplaren från Föllinge tillhöra enl. vad prof. Nannfeldt (in litt.) meddelat den nordliga typ, som bör kallas var. *lapponica* (Laest.). Det är nämligen Laestadii *O. lapponica.* Enl. docenterna Smith och Hylander ingår i min kollekt från Föllinge ett ex., som ganska säkert är *O. maculata* × *Traunsteineri* och ett, som möjligen är *O. cruenta* × *Traunsteineri.* — Alla tre arterna växa också i kärret. Dessutom förekomma typer med ofläckade blad, som torde kunna hänföras till *O. incarnata.*

Fig. 2. *Oxytropis*-lokalen på Grukksfjället. *Oxytropis* förekommer bland de mindre blocken till vänster på bilden. Foto förf. juli 1949.

Oxytropis lapponica. — Frostviken: Grukksfjället NÖ-topp c:a 780 m ö. h. Ett 20-tal individ vid basen av en gruskägla i SÖ-exposition. Confirm. E. Asplund. — I övrigt koloniseras rasmarken av bl. a. *Aconitum septentrionale*, *Asplenium viride*, *Astragalus alpinus*, *Botrychium boreale*, *Carex rupestris*, *Coeloglossum*, *Draba norvegica*, *Dryas*, *Leucorchis*, *Polystichum Lonchitis*, *Saxifraga adscendens*, *S. groenlandica*, *Trisetum spicatum* och *Veronica fruticans*. — *Oxytropis lapponica* har i Skanderna en svagt bicentrisk utbredning (jfr Hulténs atlas). Den närmaste jämtländska lokalen är Juovanjuonje i Kall (Rune 1945). Arten är således ny för Frostviken. Dess utbredningsområde har dock inte nämnvärt ändrats genom fyndet, ty arten uppträder även i sydligaste Åsele lappmark t. ex. på V. Vardofjällen (Heintze 1913). — Pressat material har överlämnats till Riksmuseet.

Peucedanum palustre. — Föllinge: vid bäcken mellan Ockertjärn och Ockern. — *Peucedanum* har i Jämtland liknande utbredning som *Ledum*, d. v. s. de flesta lokalerna ligga i urbergsområdet.

Pinguicula villosa. — Föllinge: kärr vid Hårkan SV Ockern, vid Ockertjärn, myr Ö Näsaforsen, SO om Björnpussbodarna. På alla lokalerna insprängd i fasta *Sphagnum fuscum*-kuddar.

Poa remota. — Föllinge: i granskog på platån N Nyland. Confirm. E. Asplund.

Polystichum Lonchitis. — Frostviken: Gellvernokko i SO-branterna, vid bron nära Sipmegestugan, Grukksfjället, Rörsjöns Ö-spets.

Potamogeton gramineus. — Frostviken: tjärn i reg. alp. SO riksröset 197 A. Det. E. Asplund.

Ranunculus nivalis. — Frostviken: platålandet vid Slengajaureh t.a. Växer här i täta bestånd omväxlande med bl. a. *Saxifraga oppositifolia* och *Silene acaulis.*

R. platanifolius. — Frostviken: på många ställen i Sipmegetrakten. Nordligast iakttagen vid Gaustjokk NV Raurotjuoltas stortopp i översta reg. subalp. Den ingår här i högörtäng med bl.a. *Aconitum, Mulgedium alpinum* och *Stellaria nemorum.* Lokalen torde vara landets nordligaste (jfr karta hos Fries 1949).

Rhamnus Frangula. — Föllinge: Lövsjöns SÖ strand. Lokalen meddelad av herr R. Eliasson Föllinge, som sänt förf. en kvist som belägg.

Rorippa islandica. — Frostviken: ogräs vid Jormlien. Ny för socknen.

Salix reticulata. — Föllinge: kärr nära Hårkan på Ö sidan c:a 200 m S om bron. Här även *Bartsia, Carex capillaris* och *Cypripedium.*

Schoenus ferrugineus. — Föllinge: samhällsbildande vid en tjärn strax SV om bron över Hårkan.

Sedum annuum. — Hotagen: Höberg.

Silene rupestris. — Hotagen: Höberg.

Sparganium angustifolium. — Frostviken: tjärn SO riksröset 197 A i reg. alp. Det. E. Asplund.

Trisetum spicatum. — Frostviken: Gellvernokko, Grukksfjället, Baima. Denna art, som anträffats på de flesta fjäll i nordligaste Frostviken (jfr Danielsson 1948), synes helt saknas i det eljest så rika området V om Jorm.

(*Ulmus glabra* ssp. *montana*). — Hotagen: utdöd på lokalen i sydbranten vid Höberg, enl. uppgift sedan 1945. Träden ha torkat ut, troligen på grund av de talrika inristningar, som besökare gjort i barken.

Urtica dioeca ssp. *gracilis.* — Frostviken: Jormliklumpen. Confirm. E. Asplund.

Utricularia intermedia. — Frostviken: i *Scirpus caespitosus*-kärr S om Tvärliklumpen. Det. E. Asplund.

U. vulgaris. — Hotagen: Kingens södra del. Det. E. Asplund.

Veronica Chamaedrys. — Hotagen: Höberg.

V. fruticans. — Frostviken: Grukksfjället, Gellvernokko i rasbranterna.

V. officinalis. — Hotagen: Höberg.

Viburnum Opulus. — Föllinge: vid Hårkan på V sidan N om bron.

Viola montana f. *fl. alb.* — Föllinge: vid V fästet av bron över Hårkan. Det. E. Asplund. Exemplaren ha rent vita blommor.

Summary.

Contributions to the Flora of Jämtland (Central Sweden).

A list is given of vascular plants observed during excursions in the prov. of Jämtland. Some finds are of special interest: *Carex elongata* L. was collected in northernmost Jämtland. Its Swedish nor-

thern limit was previously considered to cross the central part of the province about 100 km south of this new locality. — *Carex Hostiana* DC. This calciphilous plant was observed about 160 km north of its nearest known Swedish habitat. — *Oxytropis lapponica* (Wahlenb.) Gaud. has a minimum of frequency in the mountains of northern Jämtland. It was collected on a shale mountain in this area. — *Salix reticulata* L. is a calciphilous mountain species that rarely occurs in the lowlands. A new locality was detected in the silurean lowland-area of Jämtland.

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RUDTRÄSKET — EIN KLEINER BRAUNWASSERSEE BEI STOCKHOLM.

EINE ALLGEMEINE ORIENTIERUNG.

VON

R. W. KOLBE und A. W. SILFVERSPARRE.

Der See Rudträsket und seine nähere Umgebung wurde anfänglich von einem von uns (Silfversparre) ab 1943 zwecks Untersuchung der Moosflora vielfach besucht. Als wir dann gemeinsam (ab 1947) die Untersuchungen auch auf die Algenvegetation ausdehnten, fanden wir, dass der See für biologische Studien in vielen Beziehungen ausserordentlich günstig ist und eine reiche und mannigfaltige Algenflora beherbergt. Weitere Fachgenossen schlossen sich uns an und es ist gedacht, dass in der Folge einige Pflanzengruppen in der Form von Einzeluntersuchungen behandelt werden sollen und zwar zunächst: Moose (von H. Persson und A. W. Silfversparre), Grünalgen, Flagellaten, Cyanophyceen (von H. Skuja) und Diatomeen (von R. W. Kolbe).

Rudträsket, im Kirchspiel Huddinge gelegen, ist nur etwa 17 km in Luftlinie von Stockholm entfernt und durch eine Autobuslinie leicht erreichbar. Zwei Eigenschaften machen ihn u. A. in biologischer Beziehung interessant: seine völlige Unberührtheit und seine relativ bedeutende Meereshöhe — er liegt über der Litorina-Grenze.

Rudträsket ist ein kleiner Braunwassersee mit einer ± freien Wasserfläche von nur etwa 60 × 350 m; er bildet eine flache Wanne und der Seegrund besteht aus typischem Dy. Die Wassertiefe ist ziemlich gleichmässig in allen Teilen des Sees; die grösste Tiefe bestimmten wir in der Mitte des Sees mit 1,5 m. Rudträsket ist in einem Bruchgraben eingebettet, der in nord-südlicher Richtung verläuft und in das Becken des grösseren Sees Ådran (Kirchspiel Huddinge) mündet. Ein kleiner, etwa 750 m langer Bach, der

Fig. 1. Rudträsket, südlicher Teil, von SW nach NO aufgenommen. Am rechten Ufer Steilfelsen. Auf der freien Wasserfläche *Nymphaea-* und *Potamogeton natans*-Sozietäten. Ferner lichte Bestände von *Equisetum fluviatile*. — Phot. H. Horn af Rantzien.

in diesem Graben gelegen ist, bildet den Abfluss des Rudträsket in den Ådran.

Laut der geologischen Karte von Sveriges Geologiska Undersökningar besteht das Gestein, in das Rudträsket eingebettet ist, aus Granatgneis, d.h. dem typischen Södermanlandsgneis, der zuweilen Marmoreinlagen enthält. Die Felsen um den Rudträsket steigen — laut Generalstabskarte — bis zu einer Maximalhöhe von 94 m an. Nach den Angaben von S. G. U. wird Rudträsket im Norden von Torfdy, im Osten von Gneis, im Süden und Südwesten von Torfdy und im Westen von Gneis und Moränen begrenzt. Nur im N und SO des Sees treten die Felsen an wenigen Stellen in relativ steilem Böschungswinkel unmittelbar an den See heran; im SW-Teil des Sees geht dieser in ein ziemlich ausgedehntes Sphagnum-Moor über. Auch an weiteren Stellen (im W und N) wird der See von schmäleren *Sphagnum*-Streifen umsäumt.

Dicht am Westufer des Rudträsket unternahmen wir Bohrungen an 5 Stellen, die meistens bis zu dem Fels- oder Moränengrund hinabreichten. Die vertikale Entfernung zwischen der Seeoberfläche und dem Felsen (bezw. der Moräne) betrug 6 bis 8 m und

Fig. 2. Rudträsket, nördlicher Teil, von W nach O aufgenommen. Im Vordergrund Übergangs-Armried. *Carex lasiocarpa* das Wasser umsäumend. — Phot. H. Horn af Rantzien.

an einigen Stellen im W und SW — über 8 m. Aus technischen Gründen konnten wir nicht tiefer bohren, doch dürfte — nach der Konfiguration des Geländes zu urteilen — die Sedimenttiefe an keiner Stelle mehr als etwa 10 m betragen. Eine Bohrung am SW-Ufer ergab das nachstehende Profil:

2 m Sphagnumtorf
4 m Gyttja mit Dy gemischt
2 + m Ancylus- und Eismeerton

Also über 8 m Sediment.

Die Meereshöhe von Rudträsket war bisher nicht festgestellt worden; A. W. Silfversparre konnte sie mittels eines Nivellierinstruments bestimmen, indem er von der amtlich festgestellten Meereshöhe des Ådran ausging. Diese beträgt laut Generalstabskarte 44,3 m; Rudträsket liegt 19,3 m höher, so dass die Oberfläche von Rudträsket sich 63,6 m über dem Meeresspiegel befindet. Da die Litorina-Grenze laut den Untersuchungen von J. Schnell (1930) und S. Florin (1944) in Södertörn in einer Höhenlage von etwa 53 m.ü.M. verläuft, ist das Becken von Rudträsket von der Litorinatransgression über-

haupt nicht berührt worden, was im übrigen durch den Diatomeenbefund in unseren Bohrungen bestätigt wird und worüber in einer späteren Arbeit berichtet werden soll. Mithin dürfte Rudträsket als Süsswassersee auf ein Alter von 7000 Jahren zurückblicken — eine ungewöhnlich lange Zeit für einen kleinen Süsswassersee im Stockholmer Gebiet.

Zur Charakterisierung des Wassers von Rudträsket seien nachstehend einige Analysen angeführt:

Datum:	29.6 1948	7.9 1947	23.11 1947	29.6 1948	18.7 1948	25.8 1948	24.4 1949	14.8 1949
pH	5,93	6,10	6,10	5,93	—	5,31	—	5,74
Leitfähigkeit $\varkappa \cdot 20 \cdot 10^6$	32,9	30,0	35,5	32,9	34,0	31,0	27,4	36,4
Trockensubstanz mg/l	65,5							
Glührückstand mg/l	19,3	16	—	19,3	—	24	—	—
Ca mg/l	6,4							
Mg »	1,0							
Na »	4,3							
K »	0,8							
Cl »	9,2							
P γ/l								7,9

Zur Methodik sei das Nachstehende bemerkt:

pH, Leitfähigkeit und Glührückstand wurden nach den Methoden bestimmt, die bei Kolbe und Silfversparre (1950) beschrieben sind;

Ca wurde als Oxalat bestimmt;

Mg wurde im Oxalatfiltrat mit 8-Oxychinolin nach K. Nehring gewichtsanalytisch bestimmt. Vgl. A. Bömer, A. Juckenack, J. Tillmans: Handbuch der Lebensmittelchemie II—2, S. 1233.

K und Na wurden als Chloride und Perchlorat im Oxychinolinfiltrat bestimmt:

Chloride wurden mit Silbernitrat und Kaliumchromat titriert;

Sulfat wurde als Bariumsulfat bestimmt.

Die Wasserfarbe wurde am 6.8. 1950 nach der Platin-Kobaltmethode ermittelt und ergab einen Wert von 85 mg Pt pro 1000 ccm. Am gleichen Tage um 12 Uhr mittags betrug die Wassertemperatur +22° und der O_2-Gehalt—93 % der theoretischen Sättigung.

Zum Vergleich sei auf die Analysen von weiteren 9 Seen der Umgebung von Stockholm hingewiesen, die bei Kolbe (1950) angeführt sind. Auch diese Seen sind in Södermanlandsgneis eingebettet und die Analysen zeigen, dass der Kontakt mit diesem Gestein ein äusserst elektrolytarmes Wasser ergeben kann. Unter den erwähnten Seen nimmt Rudträsket in chemischer Beziehung eine

Mittelstellung ein: in seinem Chemismus zeigt er keine extremen Züge und dies ist vielleicht der Grund für seine reichhaltige Algenflora.

Genauere Angaben über die Kryptogamenflora von Rudträsket werden — wie bereits erwähnt — demnächst in Einzeldarstellungen erscheinen und diesen möchten wir hier nicht vorgreifen. Von allgemeinerem Interesse dürfte der Fund eines Bestandes von *Cladium mariscus* am N-Ufer des Sees sein. Ferner möchten wir erwähnen, dass eine neue, sehr charakteristische Kieselalge — *Cyclotella Arentii* — im See lebt. Sie wurde hier erstmalig beobachtet und konnte bisher nur in einigen wenigen Seen Schwedens gefunden werden, in keinem jedoch in so grosser Frequenz.

Wie eingangs erwähnt wurde ist eine vom botanischen Standpunkt wertvolle Eigenschaft von Rudträsket dessen völlige Unberührtheit von menschlichen bezw. industriellen und landwirtschaftlichen Einflüssen. Der See liegt im Kronopark, einem mit Kiefern und Fichten bewachsenen Staatsforst. Der Holzschlag wird in diesem Teil des Forstes so selten und in so geringem Umfange durchgeführt, dass von einer diesbezüglichen Beeinflussung des Sees wohl keine Rede sein kann.

Die Makrophytenvegetation[1] ist als ziemlich charakteristisch für Seen vom Typus des Rudträsket anzusehen.

Die terrestrische Stufe um Rudträsket ist von Kiefernwald beherrscht u. zw. vor allem von einem *Calluna*-Kiefernwald und von einem Felsboden-Kiefernwald. Stellenweise sind Sumpfwaldtypen anzutreffen die zur amphibischen Vegetation überleiten.

Die amphibische Stufe ist durch einen Wechsel von Hochmoor und Armried charakterisiert. Grosse Flächen an der Grenze der aquatischen Stufe, die im Wasser des Sees submergiert sind, sind von einer Vegetation eingenommen, die zu den Übergangs-Armriedern geführt werden muss. *Sphagnum apiculatum, S. dusenii, S. inundatum, S. palustre* und *S. papillosum* sind am Rudträsket die besonders charakteristischen Arten für die Bodenschicht dieser Gemeinschaft, während die Feldschicht vor allem von *Myrica gale* (zusammen mit *Carex lasiocarpa, C. rostrata* und *Menyanthes trifoliata*) charakterisiert ist. Zwischen diesem *Myrica*-Armried und der oberen Grenze der amphibischen Stufe gibt es einen Wechsel zwischen verschiedenen Armried- (meistens Extrem-Armried) und

[1] Die nachstehende Schilderung der Makrophytenvegetation von Rudträsket, die nur als eine sehr allgemeine Orientierung aufzufassen ist, wurde uns freundlichst von Fil. lic. H. Horn af Rantzien zur Verfügung gestellt.

Hochmoor-Typen. Im südwestlichsten Teil des Sees ist ein kleines trockenes, baumloses Hochmoor zu erwähnen. Seine Vegetation ist vor allem durch *Calluna, Empetrum nigrum* s. str., *Sphagnum fuscum* und *Cladonia*-Arten characterisiert. Im Westen befinden sich einige mit Kiefern bewachsene Hochmoore, deren Feldschicht von *Ledum palustre* beherrscht wird.

Die aquatische Makrophyten-Vegetation ist auf wenige Arten beschränkt und macht einen dürftigen Eindruck. Da der kleine See allseitig (mit Ausnahme einiger Stellen am östlichen Ufer) von Moor umgeben ist und da die Sedimente fast ausschliesslich aus losem Dy bestehen, zeigt die Wasserpflanzen-Vegetation grosse Ähnlichkeit mit der eines grösseren Moortümpels. Von Helophyten sind im See *Carex lasiocarpa, C. rostrata, Equisetum fluviatile, Phragmites communis*, und *Scirpus lacustris* von grösserer Bedeutung. Ausser den erwähnten Graminiden sind von Sträuchern *Myrica gale* und von Herbiden *Menyanthes trifoliata* als aquatische Komponente lokal bedeutungsvoll. In dieser Beziehung ist auch ein ausgeprägt lokales Auftreten von *Cladium mariscus* und *Typha latifolia* am Nordende des Sees zu nennen. Die Schilfe haben eine verhältnismässig grosse Ausdehnung, sind aber ziemlich licht. Von den Nymphaeiden sind nur *Potamogeton natans* und Zwischenformen von *Nymphaea alba* ssp. *candida* und ssp. *melocarpa* als gemein zu bezeichnen, während *Nuphar luteum* eine begrenzte Verbreitung in Rudträsket hat. Die *Nymphaea-Potamogeton*-Sozietäten sind im See überall zu finden; ihre Bestände sind jedoch licht. Die submerse Vegetation ist nur durch *Sparganium minimum* vertreten; die Art kommt lokal vor, erreicht aber stellenweise eine beträchtliche Dichte. In dieser Beziehung ist auch zu erwähnen, dass die Rotalge *Batrachospermum vagum* in der Unterwasser-Vegetation von Rudträsket eine grosse Rolle spielt.

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SMÄRRE UPPSATSER OCH MEDDELANDEN.

Föreningens medlemmar uppmanas att till denna avdelning insända meddelanden om märkliga växtfynd o. d.

Chromosome Behaviour in Cardiospermum Halicacabum L.

Previous work in the cytology of *Cardiospermum Halicacabum* was given by Sugiura (1936, p. 564) who published only two figures, one of the second anaphase and the other of the somatic chromosomes without any detailed explanation. The present work illustrates a brief study of the cytological behaviour of the chromosomes in somatic and meiotic divisions.

Somatic division. Number of chromosomes in *Cardiospermum Halicacabum* L. is twenty two ($2n = 22$) (Fig. 1). The chromosomes vary slightly in length. Nearly all the chromosomes have a medium centric constriction and are more or less of the same morphology. There is only one pair of chromosomes which is sharply different from the others. This pair has a trabant.

The somatic complement of 22 is a normal one in which matching of the chromosomes in pairs is possible. This indicates that the 11 chromosomes of the haploid set are duplicated without any change that would lead to an abnormal constitution.

Meiosis. The chromosomes of *Cardiospermum Halicacabum* L. are so small that critical study of the early prophase was not possible. The number of bivalents in every studied nucleus is eleven ($n = 11$) (Figs. 2—9). The maximum number of interstitial chiasmata observed at late diplotene is 7 (Fig. 3), where the number of terminal chiasmata in the same nucleus is 12. At diakinesis the highest number of chiasmata in a bivalent was found to be two which are either both terminal, or one terminal and the other interstitial.

At metaphase, the chromosomes are still further contracted. In some examined nuclei no interstitial chiasmata were observed. Fig. 7 shows nine bivalents and four univalents, this might be taken as an indication of abnormality. The case, however, on the chiasma theory of pairing, is simple, and straightforward. It may happen that two homologous chromosomes occasionally fail to form a chiasma, and these will remain as uni-

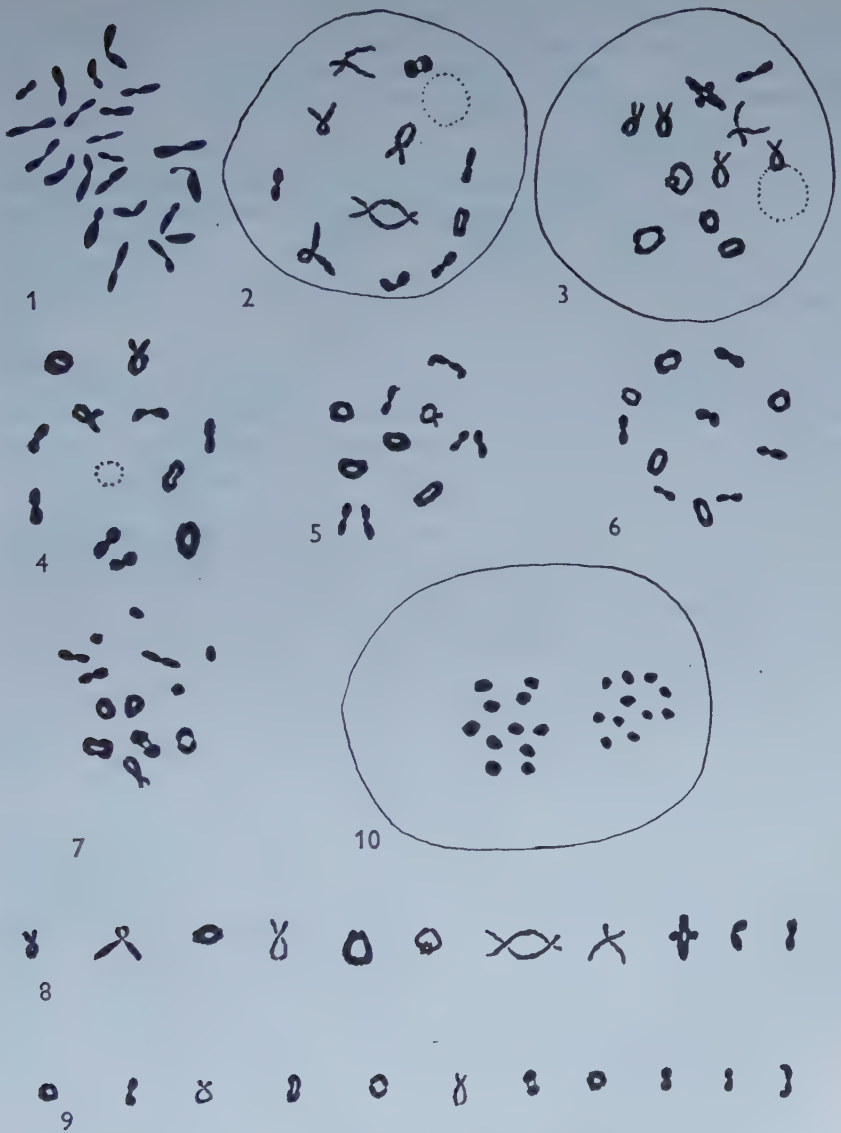

Fig. 1 Metaphase of mitosis in root tip (× 4400). — Figs. 2 & 3. Late diplotene in pollen mother cells (× 3580). — Fig. 4. Diakinesis in a pollen mother cell (× 3580). — Fig. 5. Metaphase in pollen mother cell showing eleven bivalents. In one bivalent only, an interstitial chiasma persists. Chiasmata in the other bivalents have completely terminalised (× 3580). — Fig. 6. Metaphase in a nucleus of pollen mother cell. All the chiasmata are terminal (× 3580). — Fig. 7. Metaphase in a pollen mother cell showing bivalents and four univalents (× 3580). — Fig. 8. Different types of bivalents at late diplotene in pollen mother cells. (× 3580). — Fig. 9. Different types of bivalents at metaphase in pollen mother cells. — Fig. 10. Anaphase of the first meiotic division. Each pole has received a normal haploid set of eleven chromosomes (× 3580).

valents. Univalents have similarly been observed in pure diploids (Darlington 1937) and in other diploids as in *Aconitum* (Afify 1935). In this connection it may be stated that failure of pairing is not evidence of dissimilarity between the chromosomes while, on the other hand, pairing is evidence of homology.

Fig. 9 shows the different types of bivalents met with at metaphase, comparing these types with those shown in fig. 8 for the late diplotene, bivalents clearly reveal the change which has occurred. First, the chromosomes become shorter and thicker, and second, terminalisation of chiasmata has been taking place. Consequently there are fewer chiasmata at metaphase.

Acknowledgments. The author is indebted to Professor A. Nayal, Dean of the Faculty of Agriculture, Shebin El Koam, Mr. A. Afify, the head of plant breeding section in the Royal Agricultural Society of Cairo, and Professor F. Fagerlind, Stockholm for advice, criticism and help.

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Abd El Rahman Kadry.

RECENSIONER.

Darlington, C. D., and Mather, K., Genes, Plants and People. — London (Allen & Unwin Ltd) 1950. Pris 16 s.

De båda författarna ha sammanställt ett antal uppsatser, som de, var för sig, publicerat i olika tidskrifter de senaste 20 åren (1929–1948). Man kan härigenom följa genetikens snabba utveckling under den angivna tidsperioden.

Flertalet av Darlingtons uppsatser är samlade i början av boken, men av någon anledning har två uppsatser och appendix placerats sist. Orsakerna härtill är svårförståeliga. Det hade då varit av värde att förutom tryckåret, som angivits före varje uppsats, även fått författarnamnet på grund av den ovannämnda ologiska redigeringen.

Eftersom boken skrivits under en tidsrymd av 19 år blir den automatiskt en historia. Anknytning bakåt i historien ger D. i inledningen, där han helt kort har skildrat de arbeten på hybridisering, som föregick den moderna genetiken.

De första uppsatserna behandlar 30-talets stora problem, att förena cytologi och ärftlighet. De åsikter, som där framförts, möter man i moderna läroböcker i ämnet.

I och med att de grövre dragen av kromosommekanismen blev klarlagda försköts intresset till de finare strukturerna i kromosomerna. Den kemiska byggnaden skildras klart och lättfattligt och illustreras av ett par schematiska figurer.

Förekomsten av s. k. plastogener och plasmagener beskrives kort men tydligt och är även försett med bra illustrationer. Förf. går in på en jämförelse mellan virus och plasmagener. Det är ett av de områden, där just nu en intensiv forskning pågår, varför det är vanskligt att uttala sig i ena eller andra riktningen.

I de kapitel i slutet av boken, som skrivits av D. finns ett om ärftlighet och sjukdom, som ger mycket intressanta synpunkter på både växt-, djurförädling och medicin, det senare vad det gäller framställningen av antibiotica.

D. har dessutom en artikel om populationer hos människor samt ett appendix om den ryska genetiken, skrivet före den bekanta konferensen i Moskva 1948. — Även Mather har bland sina artiklar en, som behandlar det ryska problemet.

Bland M:s artiklar finns flera, som behandlar växternas olika metoder att säkra korsbefruktning och speciellt incompatibilitet, såväl hos svampar som angiospermer.

Även M. har glidit in på frågan om genernas verkan och finare strukturer i kromosomerna. De åsikter, som där framförs, bör man inte saklöst anamma

ty här gäller det ånyo ett ämnesområde under stark utveckling. — I den sista av M:s uppsatser diskuteras problemet differentiering och kärnförändringar.

Samtliga uppsatser är försedda med litteraturförteckning, vilket i hög grad ökar deras värde.

Som helhetsintryck må sägas, att boken som ej kan kallas populärvetenskaplig, är inspirerande, ehuru ej lättläst, och eggar till läsning av ytterligare litteratur inom de ämnesområden, där expansionen är störst.

K. G. Lüning.

Fabijanowski, Jerzy, Untersuchungen über die Zusammenhange zwischen Exposition, Relief, Mikroklima und Vegetation in der Fallätsche bei Zürich. — Beiträge zur Geobot. Landesaufnahme der Schweiz, 29 (104 pp.). Bern 1950. Pris schw.fr. 13.50.

Den undersökning, vars resultat här i korthet skall refereras, har ursprungligen företagits i praktiskt syfte, närmast för att undersöka skogsavverkningens följder på vissa alpsluttningar, starkt utsatta för sommartorka och erosion. En hämningslös avverkning av dylika områden utan samtidigt insatta skyddsåtgärder har tidigare nästan varit regel; svår erosion och jordflykt har ofta framkallats härav. Speciellt avskräckande skadeverkningar har uppträtt i de sydliga kantonerna, Wallis, Tessin och Graubünden. För att studera korrelationen mellan vegetationstyper av olika slag, representerande hed-, ängs- och sluten skogsvegetation jämte alla övergångar, samt vissa av de ståndortsfaktorer, som särskilt ansågs bära ansvaret för de nämnda skadeverkningarna, företog förf. till detta arbete under 1940-talet en intensiv undersökning av ett begränsat område.

Det gällde först att med sedvanliga växtsociologiska metoder fastställa de vegetationstyper, som fanns företrädda inom området, en jättestor erosionstrichter nära Zürich. Förf. har särskilt intresserat sig för växtsamhällenas successionsförhållanden och har i enlighet därmed indelat dem i fyra stadier, av vilka Taxeto-Fagetum-skogen anses som klimaxvegetation. Inom varje stadium har hydriska och xeriska typer urskilts som varianter.

På valda punkter inom de olika växtsamhällena har nu undersökningar över vissa mikroklimatiska faktorer företagits. Vidare har varje urskild växtsociologisk enhet korrelerats till topografiska faktorer (exposition, relief). Bihangsvis har experimentella undersökningar utförts över skogsträdens föryngring inom de olika vegetationstyperna med särskild hänsyn till *Pinus silvestris* och *P. montana*, samt över den biologiska markaktiviteten (enligt Richards metod med cellulosasnören, Mitt. Schweiz. Anst. f. d. Forstl. Versuchswesen, 24, 1945).

De mirkoklimatiska undersökningarna har omfattat temperaturobservationer under längre tid (juli –oktober) och iakttagelser över dygnsvariationer samt studier över relativ luftfuktighet, markfuktighet och avdunstning. Inflytande av vegetationstäcke och nordexposition har i allmänhet yttrat sig i en nedsättning av medelvärdena hos olika klimatiska data, i mindre utpräglade extremvärden och i en förminskning av temperatur- och avdunstningsamplituder vid tilltagande fuktighet. Sydexposition och avsaknad av sluten vegetation är däremot korrelerat med uppträdande av

extremt höga temperaturer och stark uttorkning. Förf. experimentella undersökningar visar vidare att det råder vissa skillnader beträffande groningsförhållandena hos *Pinus silvestris* och *P. montana*, och att den senare arten i detta hänseende är vida mer anspråkslös. Vidare har groningsbetingelserna på sydexponerade biotyper utan starkare utvecklat fältskikt visat sig ganska olika de på nordexponerade, mer eller mindre vegetationsrika lokaler rådande. I det förra fallet har föryngringen att kämpa med stora svårigheter, åtminstone delvis på grund av starkt varierande temperatur- och fuktighetsförhållanden och på grund av diasporernas bortsköljning genom regn och tö.

Henning Horn af Rantzien.

Heimans, E., Heinsius, H. W., en Thijsse, Jac. P., Geillustreerde Flora van Nederland. Ed. 17, bewerkt door J. Heimans, A. W. Kloos Jr en G. Kruseman Jr. – W. Versluys (1180 pp, mer än 6000 figs). Amsterdam 1951. Pris

Heimans »Geillustreerde» har under det sista halvseklet i Nederländerna spelat samma roll som Lindmans flora hos oss. I sin allmänna uppläggning erinrar den något om sistnämnda arbete, men har så småningom med upplagornas mängd vuxit ut till något vida mer omfattande. I den refererade floran har praktiskt taget varje behandlad art försetts med en avbildning av en eller flera för bestämningen viktiga karaktärer. Bilderna är i de flesta fall tekniskt ganska enkla, i andra, mer utarbetade men alltid ytterst karakteristiska. En påfallande olikhet mot Lindmans flora är det mycket stora antal odlade, förvildade och adventiva arter som medtagits. Så t. ex. behandlas av familjen Commelinaceae inte mindre än sex arter (*Tradescantia virginica*, *T. fluminensis*, *Zebrina pendula*, *Commelina coelestis*, *C. tuberosa* och *C. communis*) och av dessa torde väl endast den förstnämnda ha någon utsikt att överleva de holländska vintrarna. Det mest karakteristiska för Heimans flora torde dock vara den allmänna, avslutande delen (»Bijzondere Plantkunde») till vilken ifråga om koncentration, innehåll och kvalitet det torde finnas få, om några motsvarigheter i nordiska floror. Denna avslutande del inledes med en diskussion av artbegreppet och de infraspecifika kategorierna. Den jämförelsevis utförliga framställningen bygger på moderna principer och ansluter sig närmast till av J. Huxley framförda synpunkter. Efter kortare avsnitt om bl. a. nomenklatur, fenologi, livsformer, och blombiologi följer ett starkt koncentrerat men ytterligt värdefullt växtgeografiskt kapitel vari nederländsk flora och vegetation behandlas ur historiskt, ståndortekologiskt och sociologiskt växtgeografisk synvinkel. Skildringen av de olika floristisk-växtgeografiska elementen är av största intresse. Priset tas dock av det föredömligt klara och instruktiva avsnitt som behandlar växtsociologiens teori och metodik (enligt Braun-Blanquet). Till denna senare kapiteldel ansluter sig en »Determineertabel van Nederländske Plantengemeenschappen» en bestämningstabell över de växtsamhällen av högre rang (mest allianser, stundom upptagas även associationer) vilka påträffats i nederländsk vegetation.

Henning Horn af Rantzien.

M. G. Stålfelt.

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60 ÅR

DEN 24 SEPTEMBER 1951

THERMOGROWTH REACTIONS AND GROWTH FLUCTUATIONS OF THE COLEOPTILES OF AVENA SATIVA.

BY

CARL ERMAN.

Introduction.

Every change in the external conditions which quantitatively reaches or exceeds the threshold value for the release of an irritation effects an undulatory course in the growth curve of the *Avena* coleoptile. Thus, Blaauw (1909, 1914, 1915), Vogt (1915), Sierp (1918), and others found a specific photogrowth reaction on the exposure of etiolated coleoptiles to illumination, and Tollenaar and Blaauw (1921) demonstrated a similar, though qualitatively different, response in the sporangiophors of *Phycomyces*. Later on, Dillewinj (1927) considered it necessary to distinguish between a »long photogrowth response» which is liberated on exposure of the coleoptile apex only, and a »short photogrowth response» which sets in if the subapical parts of the coleoptile are exposed to illumination. The latter response shows considerably shorter amplitudes between minima and maxima than the former.

The question whether a photo-dark-growth response (»Dunkelwachstumsreaktion») also sets in on a sudden diminution or disappearance of the illumination has, on the other hand, been more disputed.

Thus, Van De Sande Bakhuyzen (1920), Sierp (1921), and Dillewinj (1927) think they have found such a light-dark response, with its first growth maximum occurring simultaneously with the first growth minimum of the dark-light response. Brauner (1922) also considers that the growth curve, after return of the coleoptile to darkness, consists of two components, *viz.* »aus der Einwirkung des Lichtes und aus der tatsächlichen Reaktion auf die Verdunkelung».

Koningsberger (1922), on the other hand, arrived at a quite different opinion. He thinks that the response to the reduction of light intensity or to the transfer of the coleoptile into darkness is a result of the lingering after-effect of the previously released photogrowth response.

The author too (Erman 1923 a) considered it necessary to presume such an after-effect. Etiolated coleoptiles of the »*Svalövs Seger*» oats were thus exposed to shorter or longer periods (55 min. to 3 $^1/_2$ hrs.) of illumination, and their growth curve was observed for some time. It was evident from this that the undulatory progress of growth resulting from the illumination continued after the transfer of the experimental material into darkness. On interruption of the illumination in or near a minimum of the photogrowth curve (as in curves II, IV, and V, table 9, p. 348), a seeming light-dark response, with a primary maximum and a subsequent minimum was obtained. If, on the contrary, the illumination was discontinued in or near a maximum, a minimum was first obtained and after that a maximum. In both cases there was obviously an after-effect of the preceding photogrowth response. The occurrence of such a »light-dark response» was then of special interest in the animated contest for or against Blaauw's theory, *i.e.* for the interpretation of the phototropic curvatures (cf. Bremekamp 1918, 1921, Brauner 1922, Lundegårdh 1922, Nuernbergk 1927, *et al.*). The question has afterwards assumed another aspect through the investigations on the chemical growth factors and their importance for the phototropic phenomena (cf. Filtzer 1929, van Overbeck 1933, 1936, Borgström 1939, van Guttenberg 1942, *et al.*).

A geogrowth response reminding of the photogrowth response was found by Zollikofer (1922). This geogrowth response was supposed to manifest itself on the one hand in the change of the uniform earlier growth into an undulatory one, on the other hand in an average increase in the general rate of growth followed after a time by an inhibition of growth, however. Dolk (1930) has afterwards denied the occurrence of such a response — as far as the *Avena* coleoptile is concerned at least.

A specific hydrogrowth response occasioned by a sudden change in the humidity of air was observed by Walter (1921) in the sporangiophors of *Phycomyces*, and a similar one may be assumed in the *Avena* coleoptile (Erman 1926).

Lastly, Silberschmidt (1925) and the author (1926) have, in-

dependent of each other, shown a thermogrowth response in coleoptiles of *Avena*, *Hordeum*, and *Triticum* as well as in the hypocotyl of *Linum*.

After SILBERSCHMIDT and I published our scanty investigations on this reaction none more have appeared as far as I am aware.

In order to get a somewhat widened insight into the progress and nature of the last-mentioned response, I resumed my investigations on it in 1946. They were carried out at the Botanical Institute of the University of Stockholm, where Professor M. G. STÅLFELT most kindly assigned a place to me in his laboratory, placed the requisite apparatuses at my disposal, and in every way supported and encouraged me in my work.

Experimental Arrangement.

In the present investigation on the thermogrowth reaction the specially constructed thermostat reproduced in fig. 1 was used. It has earlier been employed in my investigation on the photogrowth reaction (ERMAN 1930) and was described in that connection. It was built after my design in the workshop of LINDELÖF Bros, mechanicians, at Lund.

All the apparatuses were placed in a spacious dark-room provided with an effective light-sluice and ventilating device. Coleoptiles of *Avena* sativa were the only subjects employed, and the material consisted of pure lines of resp. the »Svalövs Seger» oats and the »Svalövs Primus» oats, both from the *élite* of 1945.

The methods used in the experiments were as follows:

The peeled fruits of the resp. races of oats were transferred into Petri dishes, where they were left to swell for about 24 hrs. Only grains with normally developed endosperm were used, as it became evident that the heaviest grains by no means gave a coleoptile length proportional to the weight of the grains, a fact observed also by HAMADA (1931, p. 178) *int.al.* The swelling took place in daylight in order to inhibit the mesocotyl growth.

Planting-out was made according to the wet method.

Slides with slips of coarse filter-paper wound three times round them were put down into preparation tubes 4 cm in diameter, 7 cm in height, and filled with tap water. The slides obtained an inclination of about 5° in the tubes.

Before the slides were placed in the tubes a triangular opening

was made at the anterior (upper) edge of the filter-paper by means of a pair of tweezers, and in this opening the soaked grain was inserted with its plumular side turned outward (forward). With about half its length sticking out of the opening the grain was accurately orientated in perpendicular direction. For in most cases where there was too small an opening in the filter-paper, too deep an insertion or only an oblique position of the grain, the growing coleoptile would try to find its way under the edge of the paper and out to the side of the glass.

In the course of the experiments 8 to 10 such tubes were made ready every day and after 4 to 5 days when the coleoptiles had reached the desired length the selected experimental tubes were placed in the thermostat, where they were left under constant external conditions till next day, when the experiments began.

Two horizontal microscopes of different make and different optical properties were used for growth measurements. By adjustment of the tube, exactly the same enlargement was attained on checking with an object micrometer. A 1/10 dividing line on the scale of the ocular micrometer was then found to correspond to 8 μ. This measure is the unit used in all the tables on elongation.

Two phototropically inactive, red, 15-watt dark-room lamps were placed behind the thermostat. They were continuously on. The windows of the thermostat also consisted of red ruby glass.

The horizontal microscopes were carefully adjusted in the vertical and lateral directions, and the readings were as a rule made at intervals of 5 min. and with an aberration of 10 sec. at the most.

The preliminary investigations showed that the placing of the preparation glasses on the floor of the thermostat implied a serious source of error, which was simply due to the thermal expansion of the thermostat material as such. An attempt to eliminate this source of error by the employment of radiators hung up in the plate cylinders miscarried.

After various experimental arrangements without the desired effect, a simple method for elimination of the said source of error was finally found.

Thus, two double-twisted threads of paper-yarn about 1 mm thick were fastened to the ceiling inside the respective observation windows by means of so-called tacks. Small curtain-holders were attached to the lower ends of the threads. The length of the threads was adjusted so that the slide would hang clear of the preparation tubes when the

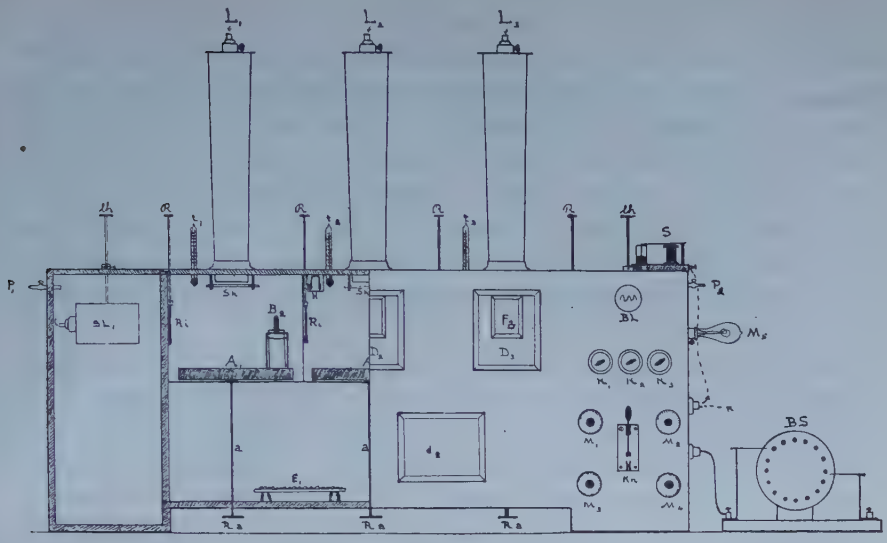

Fig. 1. Thermostat for tropistic experiments. (Acc. to ERMAN 1930.)

holders were made fast about 1 cm below its upper edge. The elongation of the selected kind of thread on heating now corresponded exactly to the expansion of the thermostat material in the opposite direction within all the intervals of temperature employed, a fact which was carefully controlled by repeated blank trials.

By this experimental arrangement straight-growing coleoptiles free from any considerable nutations were obtained, only a few of which had to be ruled out.

The Thermogrowth Reaction in the resp. Coleoptiles of the Primus Oats and the Seger Oats on different Temperature Rises.

As, from a purely quantitative point of view, SILBERSCHMIDT's and my own investigations on the thermogrowth reaction showed an aberration in certain values, a more detailed study of the cause of this aberration was required. A series of preliminary experiments with different rise in temperature at varying length of coleoptiles were performed for this purpose. In all these experiments the bottom radiators of the thermostat were used. A series of experiments, with employment of the radiators suspended in the cylinders L_1—L_3 (fig. 1) revealed great difficulties to center accurately at the apices of the coleoptiles, which too often resulted in thermotropic curvatures.

Therefore the built-in proper radiators of the thermostat were the only ones made use of. By readjustment of the thermoregulator the maximum rise in temperature gradually increased in the various series of experiments. The temperature readings took place at intervals coincident with those of the growth readings. In the tables on the other side, however, only the initial temperature and the maximum temperature rise are stated. The approximate point of time for the latter is indicated by its place in the time column. After having attained this maximum value the temperature remained relatively constant ($\pm$ 0.2°).

The first line in the tables states the growth during the resp. 5-min. intervals. It is expressed in the number of 1/10 dividing lines (= 8 μ). The next line shows the average value of growth for each half-hour, while the third and last one states the resp. initial temperature and maximum rise in temperature. (C. l. = length of coleoptile in mm.)

Table I shows that the appearance of the growth curve initiated by temperature rise is greatly varying in the separate experiments. On a protracted influence of temperatures of about 50° C growth is almost completely inhibited and collapse contractions ensue.

It may be noticed as a common feature, however, that the growth of the coleoptiles as a rule shows a distinct maximum about 10 to 20 min. after the initiation of the temperature increase. Sometimes, however, this maximum will occur already after 5 min. and in other cases its position is difficult to ascertain.

A still more variable position has the first minimum of the thermo-growth reaction. By collecting the average values of all the experiments included in table II, however, a relatively clear idea of the growth curve course as well as of the resp. maximum and minimum is obtained. Such a tabulation also eliminates the influence exerted in the separate experiments by the growth fluctuations normally occurring in the coleoptile.

Thus, the sudden temperature increase gives rise to a distinct maximum after about 10 min. Quantitatively the increase amounts to nearly 100 per cent of the average growth intensity before the temperature increase. This first maximum is succeeded by a relative minimum after about 50 min. The latter, however, is less pronounced and never sinks to the value before the increase in temperature.

As the »Svalövs Seger» oats had been the subject in my own as well as in Silberschmidt's earlier investigations, a series of ex-

Table I. The thermogrowth reaction in the »Svalövs Primus» oats on different sudden temperature rises (↓ = temp. rise).

C.I. 14:	6	6	6	7	6	8	↓	6	8	11	11	8	7	9	6	10	7	7	10		
			6.5								8.5					8.2					
					16.3°		+ 3.4°														
» 17:	5	5	5	6	6	5	↓	6	4	9	7	6	5	7	6	9	5	6	7		
			5.3								6.2					6.7					
					16.3°		+ 3.4°														
» 15:	4	4	2	2	1	2	↓	5	5	4	3	2	3	3	1	2	2	3	3		
			2.5								3.7					2.3					
					19.1°		+ 3.4°														
» 28:	4	6	6	6	8	5	↓	5	5	7	10	8	7	4	6	5	7	7	7		
			5.8								7.0					6.0					
					19.1°		+ 3.4°														
» 18:	9	5	7	7	5	7	↓	10	9	8	7	9	8	8	7	6	7	8	6		
			6.7								8.5					7.3					
					19°		+ 4°														
» 21:	6	9	5	7	8	8	↓	10	12	11	10	10	10	11	10	9	10	9	8		
			7.2								10.5					9.2					
					19°		+ 4°														
» 13:	7	9	5	5	5	4	↓	5	7	4	4	7	4	8	9	9	4	7	8		
			5.8								5.2					7.5					
					18.2°		+ 4.8°														
» 28:	8	7	5	7	7	8	↓	10	9	11	11	11	10	10	10	10	6	8	9		
			7.0								10.2					9.2					
					18.2°		+ 4.8°														
» 14:	5	4	5	4	3	4	↓	4	12	11	9	7	3	3	5	7	8	8	8		
			4.2								7.7					6.5					
					19°		+ 5°														
» 33:	9	9	10	12	10	13	↓	12	17	10	12	11	10	10	10	10	11	11	11		
			10.5								12.0					6.5					
					19°		+ 5°														
» 12:	6	3	3	5	3	2	↓	2	3	9	8	8	8	6	4	5	6	6	5		
			3.7								6.3					5.3					
					17.2°		+ 5.8°														
» 21:	3	3	4	3	5	3	↓	5	9	6	5	5	8	5	4	2	3	3	3		
			3.5								7.1					3.7					
					17.2°		+ 5.8°														

C.l. 18:	4	6	4	5	5	8	↓	6	9	12	12	12	5	6	8	4	7	5	5
			5.3								6.2					5.8			
					19.3°		+ 6°												
» 22:	6	7	9	9	9	9	↓	10	15	10	8	13	11	8	12	9	9	11	10
			8.0								11.2					9.8			
					20°		+ 6°												
» 26:	7	9	8	9	9	7	↓	10	7	8	14	14	13	11	10	18	9	10	7
			8.2								12.7					9.2			
					20°		+ 6°												
» 5:	2	1	5	2	3	3	↓	4	9	2	4	3	1	4	2	3	1	4	4
			2.8								6.0					3.7			
					19°		+ 6.2°												
» 14:	5	4	7	5	6	3	↓	8	15	12	9	9	8	10	9	5	8	7	5
			5.0								12.0					7.3			
					19°		+ 6.2°												
» 8:	5	4	2	6	7	4	↓	8	10	5	4	2	3	4	3	1	5	3	2
			4.7								6.2					3.2			
					20°		+ 6.5°												
» 17:	9	6	6	9	5	6	↓	9	11	10	13	11	9	10	9	8	8	8	9
			6.7								10.5					8.7			
					20°		+ 6.5°												
» 13:	4	5	5	5	5	4	↓	6	7	4	5	4	5	5	5	6	4	8	4
			4.7								5.2					5.3			
					21°		+ 7.5°												
» 23:	11	11	10	7	9	7	↓	6	10	8	10	10	10	11	12	14	9	11	12
			9.2								9.8					11.5			
					20.2°		+ 7.5°												
» 12:	2	3	3	4	1	4	↓	10	10	10	2	0	2	6	2	3	4	3	4
			2.8								6.2					3.7			
					19.6°		+ 9.5°												
» 22:	6	11	7	9	9	8	↓	14	10	11	11	13	12	11	10	10	8	6	9
			8.3								11.7					9.0			
					19.6°		+ 9.5°												
» 19:	10	14	11	14	11	12	↓	9	14	13	10	11	13	14	10	11	11	13	10
			12.1								12.7					11.5			
					22.2°		+ 10.3°												
» 14:	7	3	7	5	6	8	↓	8	16	17	15	8	7	6	8	6	4	7	8
			6.0								11.8					6.5			
					14.1°		+ 12.4°												

C.l. 8:	2	1	2	3	1	1	↓	2	6	10	10	6	1	0	0	0	1	5	1
			1.7								6.3					1.2			
					13.1°		+ 14°												
» 15:	3	4	5	5	6	5	↓	5	7	10	11	15	10	0	4	10	12	10	11
			4.7								9.7					7.8			
					13.1°		+ 14°												
» 24:	4	4	5	4	4	4	↓	8	21	20	16	9	8	5	5	5	5	3	7
			4.0								13.7					5.0			
					11.6°		+ 20.9°												
» 25:	4	5	4	6	3	4	↓	10	16	10	9	12	12	9	8	8	7	5	8
			4.3								11.5					7.5			
					11.6°		+ 20.9°												
» 6:	4	4	6	4	4	6	↓	9	9	6	10	14	13	10	11	6	6	4	0
			4.7								10.2					5.7			
					17.2°		+ 22.8°												
» 19:	5	5	2	5	5	6	↓	8	9	11	11	11	9	10	3	7	2	6	–4
			4.7								9.8					4.0			
					17.2°		+ 22.8°												
» 11:	3	3	4	5	3	3	↓	4	10	12	12	10	7	–3	–11	–2	–1	0	0
			3.5								11.7					–2.8			
					14.5°		+ 24.5°												
» 17:	4	3	4	5	5	4	↓	2	8	8	7	11	8	9	7	9	8	7	7
			4.2								7.3					7.8			
					14.5°		+ 24.5°												

Table II. Average values of the thermogrowth reaction in coleoptiles of the »Svalövs Primus» oats at temperature rises of between 3.9° and 22.7° C (33 experiments).

Average value per 5 min.	5	10	15	20	25	30	35	40	45	50	55	60 min.
before temp. rise 5.5 ↓	7.6	10.7	10.4	10.1	9.0	7.8	6.8	6.2	6.4	6.1	7.6	6.3

Table III. Average values of the thermogrowth reaction in coleoptiles of the »Svalövs Seger» oats at temperature rises of between 4° and 8° C (13 experiments.)

Average value per 5 min.	5	10	15	20	25	30	35	40	45	50	55	60 min.
before temp. rise 7.0 ↓	8.8	9.8	9.7	9.5	6.1	6.6	6.1	6.8	6.8	8.2	8.0	7.6

periments were performed with this pure strain also, the results of which are collected in table III.

Fig. 2 shows the progress of the growth reactions in both races (»Primus» = solid line, »Seger» = dotted line).

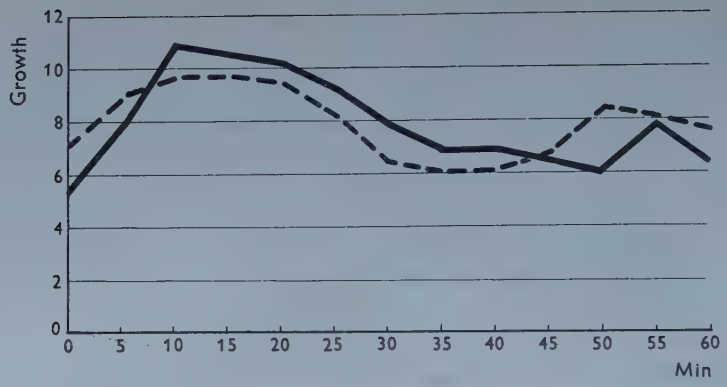

Fig. 2. The course of the thermogrowth reaction in the resp. »*Svalövs Primus*» oats I (solid line) and »*Svalövs Seger*» oats (dotted line).

A comparison between the two races shows that the »Seger» oats has an earlier minimum, *viz.* about 30 min. to about 50 min. for the »Primus» oats. The latter strain also appears physiologically more sensitive to irritants, with a stronger response.

In the series of the »Seger» oats was the average tempearture before the temperature rise 19.2° and the average value of the temperature rise 6.5°. If we select from table I the experiments covering a temperature rise from 4.8° C to 7.5° C inclusive, these 15 experiments show a pre-experimental temperature averaging 19.5° C and an average rise in temperature of 6.2° C. Thus, the values obtained admit of a direct quantitative comparison. This shows that, in spite of the higher pre-experimental growth tonicity (7.0) of the »Seger» oats, their first growth curve maximum exceeds this average value with 40 per cent only, while the corresponding value for »Primus I» amounts to 70 per cent. Thus, the two strains differ quantitatively as well as qualitatively in physiological irritability.

In my earlier investigations of the photogrowth reaction in various races of *Avena* (Erman 1930) I could demonstrate a similar state of things. Table IV below is taken from these investigations (p. 208). It includes 6 different races of *Avena* and the reading intervals amount to 3 min. ($\downarrow$ = begin of exposure).

Accordingly, of these pure strains the »Eko» oats show a very early minimum (already after 18 min.) while the maximum comes rather late, or at 51 min. The races »1752», »Fortuna», and »Stormogul» have all of them their first minimum after 21 min., the first one its maximum after 45 min., while the other two have theirs

Table IV. The photogrowth reactions in 6 different races of Avena.

Race	Number of experiments	Average length, mm	3	6	9	12	15	18	21	24
Eko	24	25	17.8	18.0	17.9	17.8	17.7	18.1	18.1	18.0
1752	18	19	11.1	11.0	11.0	11.4	11.2	11.3	11.0	11.0
Fortuna	21	24	15.9	16.1	16.2	15.8	15.9	16.5	16.6	16.9
Stormogul	24	17	19.2	17.8	18.4	17.5	17.4	18.6	17.3	18.7
Argus	10	19	12.6	12.8	12.0	12.6	12.6	12.7	12.8	12.6
Seger	12	19	10.4	10.1	10.8	10.2	10.9	10.9	10.7	10.3

Race	3	6	9	12	15	18	21	24	27	30	33
Eko	24.4	20.8	20.3	21.6	15.5	*11.8*	13.3	16.1	20.4	21.8	23.3
1752	14.8	14.1	14.0	12.6	9.6	8.4	*7.5*	8.1	12.0	14.1	14.0
Fortuna	19.9	17.7	17.3	16.5	14.7	14.7	*11.3*	15.3	17.0	17.8	*23.4*
Stormogul	16.9	16.2	14.3	14.8	14.5	14.0	*10.4*	11.2	18.2	28.0	*28.4*
Argus	12.6	15.8	12.8	13.6	13.8	12.6	11.2	*11.1*	13.8	15.3	15.1

Race	36	39	42	45	48	51	54	57	60
Eko	26.9	29.0	28.9	29.1	29.8	*30.6*	26.3	20.0	17.3
1752	14.0	13.6	14.9	*16.8*	13.9	12.0	14.4	11.6	12.3
Fortuna	*23.4*	23.1	19.5	19.1	17.4	16.4	19.7	18.6	16.7
Stormogul	22.0	21.3	23.4	22.8	21.1	21.6	21.0	21.1	20.8
Argus	18.2	24.5	24.2	18.0	14.2	9.1	8.6	9.8	11.2
Seger	14.4	11.3	11.6	14.0	13.2	13.1	*16.0*	*16.0*	12.6

already after about 33 min. »Argus» and »Seger», lastly, have late minima after 24 and 27 min. respectively, and the maximum of »Seger» does not occur until after 54 to 57 min.

This considerable variation in the different races shows the necessity to take into account which race of the experimental material has been used in every qualitative as well as quantitative comparison between the results of different authors.

Remarkable in this connection is the sudden increase in growth that is noticeable in some of the races immediately after the exposure has begun. It is specially striking in »Eko», where it amounted to no less than 35 per cent of the growth value for the same interval of time before the exposure.

A more detailed study of the exact point of time for the increase of growth revealed that this occurred already during the first minute after the etiolated coleoptile had been exposed to illumination. A collection of the results of a few experiments with »Eko» oats (average values from 4 experiments) are given in table V. Reading interval 1 min.

Table V. The exact point of time for the increase of growth in the photogrowth reaction.

Minutes	1	2	3	4	5	1	2	3	4	5	6	7	8	9
Growth values	1.6	1.5	1.7	1.5	1.6 ↓	*2.3*	2.0	1.8	1.9	1.7	1.6	1.7	1.6	1.7

Thus, the growth increase is immediately noticeable after the initiation of the illumination and has its maximum during the first minute. In control experiments with coleoptiles killed with Carnoy the reaction entirely fails to appear. It is also connected with the growth as such. Whether this sudden increase in growth should be regarded as a part-component of the subsequent photogrowth reaction or not, is difficult to decide. It was noticeable not only at high light intensities and continuous illumination but also at very low intensities and times of exposure of only a sec. or so.

Thermogrowth Reactions in the Avena Coleoptile on alternate increase and decrease in temperature.

According to SILBERSCHMIDT (1925, experiment 4) a thermogrowth reaction would appear on a sudden decrease in temperature also. It begins — quite as a temperature increase — with a maximum, which after a time is followed by a minimum.

SILBERSCHMIDT observed the growth of an *Avena* coleoptile at a temperature of +15° C for 40 min. Thereafter the temperature was lowered to +5.5° C, where it was kept for 2 $^1/_2$ hr., whereupon it was raised again to +15° C. He then obtained the following growth values (expressed in μ in readings at 5-min. intervals):

100 128 100 114 100 114 114 ↓ 28.5 *57* 43 43 *28.5* *28.5*
28.5 28.5 28.5 28.5 28.5 28.5 28.5 43 43 57 28.5 57
57 28.5 57 28.5 57 28.5 28.5 28.5 28.5 28.5 ↑
85.5 *142.5* *142.5* 114.5 114.0 57 57 57 57 57 *28.5* *28.5*
57 57 85.5 85.5 85.5 85.5 71 71 85.5 114 85.5 100

SILBERSCHMIDT is inclined to interpret the growth value 57 (10 min. after the temperature decrease) from the values thus obtained, as a maximum corresponding to the maximum which occurs 10 min. after the temperature increase effected afterwards and which is in this case represented by the value 142.5 μ. The first maximum lies about 50 per cent lower, certainly, than the average value of growth before the decrease in temperature (111 μ) which, however, might

be referred to the general decrease in growth due to the decrease in temperature.

The value 28.5 after 25 min. SILBERSCHMIDT is inclined to regard as a minimum. Immediately after the decrease in temperature, however, we find the same value, which moreover lies rather close to the average value for the whole of the cold period (= 37 μ); it may be incidentally remarked that SILBERSCHMIDT states this to comprise 2 $^1/_2$ hr. while in reality he only makes 28 readings. Also, the readings preceding the temperature decrease correspond to a period of 35 min., not to the stated 40 min.

In the table constant growth values for more than 30 successive min. are to be found, which is no doubt a very rare occurrence at a thermogrowth reaction. Thus, the author himself has never, in spite of hundreds of trials, found such a long stability in the growth values after a change in the external conditions. Another remarkable fact is that the average growth per 5 min., which before the decrease in temperature amounted to 111 μ and during the cold period to about 37 μ, after restoration of the higher temperature did not exceed 78 μ, in spite of the observations being extended over a space of 115 min.

As the question of the occurrence of a reaction of the above described kind was worth a revision the following experiments were made:

In the two partitions of the thermostat experimental coleoptiles were placed while the middle partition was shut off by the curtains (Ri in fig. 1). In the middle partition was the thermoregulator, which consequently was readjustable for different temperatures without disturbing the subjects. In all the experiments the coleoptiles were under constant temperature and otherwise constant external conditions för 24 hr. at least, before the experiments started.

In table VI on the other side the first line presents the time intervals for the readings, the second resp. the fourth line the growth values read during them, and the third resp. the fifth one the average growth per 5 min. for each halfhour interval. In the bottom line the temperature is stated.

The coleoptiles used in the experiments were of the same age and showed about the same growth intensity (4.0 and 4.3 resp. per 5 min.) before the beginning of the experiment. In the first temperature increase the temperature rises with 20.4° to 32° C within 15 min. As might be expected (*cf.* p. 426) this rise in temperature causes a growth maximum after 10 to 15 min. This is succeeded by a slow

Table VI. Thermogrowth reactions in coleoptiles of the »Svalövs Primus» oats on sudden changes in temperature (↓ = temp. increase, ↑ = temp. decrease).

																							Average growth per 5 min. for one hour
C. l.	5	10	15	20	25	30	5	10	15	20	25	30	35	40	45	50	55	60	
24 mm	4	4	5	4	4	3	8	11	12	10	9	8	8	7	6	8	7	9	
			4.0						9.3						7.5				12.1
25 mm	4	5	4	6	3	4	9	16	15	9	8	9	9	8	9	7	9	8	
			4.3						11.0						8.3				11.8
Temp.	11.6°				11.6°	↓	21°		32°				27°				27°		

	5	10	15	20	25	30	↑	5	10	15	20	25	30
	11	12	14	15	17	13		11	11	11	11	8	7
			13.7							9.8			
	12	13	15	14	12	12		17	16	11	14	10	10
			13.0							13.8			
	27°					27°		22°		21°			20.5°

	5	10	15	20	25	30	↑	5	10	15	20	25	30
	21	16	10	14	13	13		9	5	7	6	4	9
			14.5							6.7			
	17	16	11	14	12	12		9	7	7	10	11	6
			13.7							8.3			
↓	30°					28°		24°		22°			20°

decrease to a minimum after 45 to 50 min., followed by a new growth rise. The average growth per 5 min. before the temperature increase was, as mentioned, 4.0 and 4.3 for the resp. coleoptiles. During the first 30 min. in the higher temperature these values have risen to 9.3 and 11.0 respectively and thereafter sunk back to 7.5 and 8.3 respectively. The subsequent 60 min. mean an adaptation to the higher temperature (27°), with growth values of 12.1 and 11.8 respectively.

After the temperature has thus been kept constant for about 2 hr. it falls by 6.5°. The growth curves of both the coleoptiles are at this time on their way to a minimum in the growth oscillation effected by the preceding temperature rise. For coleoptile nr 1 no influence whatever on the regression can be traced after the temperature fall, and the rise in growth noticeable in coleoptile nr 2 also falls within the bounds of possibility for an after-effect of the preceding rise in temperature, for only the position of the first maximum seems to be exactly timed within one and the same race (*cf.* fig. 3).

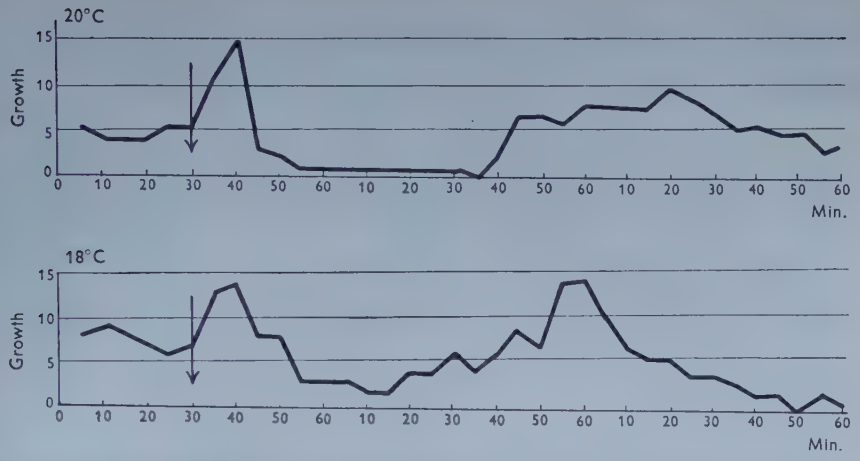

Fig. 3. The undulatory course of the thermogrowth curve for coleoptiles of the »*Svalövs Primus*» oats at a sudden temperature rise of 18°—20° C.

A subsequent sudden temperature rise of 9.5° immediately gives a new maximum, while a temperature fall setting in 30 min. later does not leave any trace in the expected growth curve.

Various similar experiments were performed but in no case could a sudden increase of growth be established after a temperature fall. After the rise in temperature, however, the growth reaction proved to consist of several successive maxima and minima. Fig. 3 presents one of the experiments that show this undulatory course of the thermogrowth reaction.

Both the growth curves of the coleoptiles, then, show their first maximum after 10 min. Another is noticeable for coleoptile nr 1 after 110 min., for coleoptile nr 2 already after 90 min. The second maximum can often reach the same height as the first one, or even exceed this (quite as in the photogrowth reaction).

It could further be established as a general rule that the value of the first maximum of the thermogrowth reaction in one and the same strain is directly proportional to the effected temperature rise.

This is evident from table VII which is composed of a number of experiments with different temperature rises.

In the last column of the above table the average value of the temperature rise has been multipled by 10 and the product obtained has been divided by the per cent number for the growth increase in the first maximum of the growth curve. In spite of the relatively

Table VII. The ratio of the temperature rise to the value of the first maximum in the thermogrowth curve for coleoptiles of the »Svalövs Primus» oats.

Number of experiments	Intervals of temp. rise, °C	Average value, °C	Average growth	Average height of max.	Growt increase in max., %	Quotient of temp. rise × 10/growth increase
8	3.4— 4.8	3.9	5.85	8.1	38	1.03
13	5.0— 7.5	6.2	6.88	11.1	61	1.02
16	9.5—14	11.6	6.0	13.3	120	0.97
16	20.9—24,5	22.7	4.2	13.3	217	1.05

small number of experiments (each as a rule with two subjects) a constant ratio of the temperature rise to the value of the first maximum is obtained.

The magnitude of the growth rise in the first maximum of the thermogrowth curve is on the contrary independent of the length of the coleoptile. This is seen from table VIII. This table presents the values of the growth increase for all the coleoptiles below 20 mm in length as well as of such that have attained 20 mm and more.

Table VIII. The ratio of the value of the first growth curve maximum to the coleoptile length (Primus oats).

Average length of coleoptiles, mm	Average value of temp. rise, °C	Growth increase in max. in per cent
12.7	6.2	69
25	6.1	70

Consequently, every suspicion of a purely physical extension phenomenon is refuted.

As I have pointed out in my earlier investigations on the thermogrowth reaction (Erman 1926) this reaction probably covers a simultaneous hydrogrowth reaction initiated by the increased relative humidity, for in all the experiments performed here in the thermostat this rises simultaneously with the temperature from originally between 50 and 65 per cent to between 80 and 95 per cent. By a special arrangement with detached coleoptiles in the experimental room and by heating by means of a quite inconsiderable heating resistance placed above the apex of the coleoptile it was pos-

sible to keep the relative humidity of the experimental room constant in the course of the experiment, but this arrangement does not exclude a change of the humidity in the air layer close about the coleoptile.

Neither do the growth reactions obtained by this arrangement deviate qualitatively from those produced in the thermostat. A quantitative comparison between the maximum value for a given temperature rise at a resp. increased and constant room humidity shows, however, that the growth values for the maximum on a simultaneous rise of humidity and temperature are often 50 per cent higher than at a rise of temperature only.

Thus, these experiments seem to confirm my earlier observations in which I found considerably more pronounced maxima and minima in the experimental series where the air humidity was simultaneously increased, in comparison to the series with constant humidity. SILBERSCHMIDT (1925), I regret to say, says nothing about the variations in humidity in his experiments.

The Growth of the Avena Coleoptile under Constant External Conditions.

Already ZOLLIKOFER (1922, p. 249) supposes that not even under constant external conditions is the coleoptile growth continuous. »Der Wachstumsansteig der grossen Periode, der deutlich zum Ausdruck kommt, wird nicht in gleichmässigen Fortschreiten erreicht sondern in einer deutlichen Wellenbewegung.»

The course of the curves in my own investigations (ERMAN 1923 a, tables 1—8, p. 338—345) also backs up the supposition that, besides the light component, an additional component takes part in the formation of the growth curves.

The undulatory progress of growth has also previously been the subject of discussion, *viz.* in connection with the question of the influence of the gravity component on the growth of the orthotropic organs. Already NOLL (1892) took up this problem. He arrived at the opinion that an organ, the longitudinal axis of which coincides with the radius of the earth is in an unirritable position with regard to gravity. PFEFFER (1893), on the other hand, considers that gravity also in this seemingly neutral position exerts a geotropic irritation. Later investigations by RICHTER (1894), RACIBORSKI (1900), and

Hering (1904) have shown that a distinct retardation of the elongation appears on inverse influence of gravity. Romell-Riss (1914) found a retarding effect of gravity acting in longitudinal direction of *Lupinus* roots, while Koningsberger (1922) demonstrates a growth increase in the coleoptiles of *Avena* arising under the same conditions.

I myself have earlier (Erman 1923 b) studied the influence of the gravity component on the progress of growth in the same subject. While Zollikofer and Koningsberger had in their investigations studied the growth of coleoptiles which, after having been adapted to the vertical position had been transferred to horizontal rotation, I myself worked at plants which from the initiation of germination were placed on the clinostat. Table IX below is taken from these investigations (table 4, p. 427).

As is clearly evident from the table, the growth of a coleoptile which has been relieved of the longitudinally acting gravity component has an undulatory course. This growth oscillation cannot have been initiated by the radially directed gravity, for partly has the coleoptile been allowed from the very beginning of growth to develop under horizontal rotation, and partly has the time of revolution been kept at $2\,^1/_2$ and $1\,^1/_4$ min. respectively, *i.e.* times shorter than the geotropic time of exposure for the subject in question. According to the statement of Rutten-Pekelharing (1910) this amounts to $4\,^1/_2$ min. at an angle of 90° and a temperature of 22.5° C.

On scrutinizing the separate curves with respect to the position of the coleoptile in »the long period», we find shorter intervals between maxima and minima and a slighter response than in the vicinity of the optimum of the period. The latter Koningsberger states for the »Seger» oats to be situated at a coleoptile length of 34 mm on an average. In the descending part of the »long period» the width of fluctuation diminishes again successively and the length of intervals becomes shorter.

Here, then, it is a question of periodicity in the growth intensity of the coleoptile for which no external, releasing factors can apparently be made responsible.

When the vertically placed coleoptile is under the influence of the gravity component this seems to act equalizing on the autonomous growth oscillations, but is this equalizing power neutralized the pendular course vill reappear.

Table IX. Periodical oscillations in the growth of the *Avena* coleoptile at horizontal clinostat rotation (Svalöv's Seger oats).

Length of the col., mm	Time of revol., min.	Temp., °C	%	5	10	15	20	25	30	35	40	45	50	55	60	5	10	15	20	25	30	35	40	45	50	55	60	Intervals, min.
5	$1\,^1/_4$	18.5	—	0.3	**0.4**	0.3	0.3	*0.2*	*0.2*	0.3	0.3	**0.4**	0.3	0.3	0.3	*0.2*	0.3	0.3	**0.4**	**0.4**	0.3	0.3	0.3	0.3	0.4	**0.5**	0.4	35
8	$1\,^1/_4$	16.8	—	0.5	0.5	**0.6**	0.5	0.5	*0.4*	*0.4*	0.5	0.5	**0.6**	0.5	*0.4*	*0.4*	0.5	0.5	**0.6**	0.5	0.5	*0.4*	0.5	0.5	0.5	**0.6**	0.5	35
12	$1\,^1/_4$	19.7	—	0.9	0.8	*0.4*	0.6	0.9	**1.7**	1.3	1.0	0.6	*0.4*	0.5	1.0	**1.6**	1.3	0.8	*0.5*	0.6	0.7	**1.0**	0.6	0.5	0.5	0.7	1.0	30—35
13	$1\,^1/_4$	17.6		0.4	**0.6**	0.5	*0.3*	*0.3*	0.4	0.4	0.5	0.6	**0.7**	0.5	0.5	0.4	*0.3*	*0.3*	0.4	0.5	**0.6**	**0.6**	0.5	0.4	*0.3*	0.4	0.4	40
14	$1\,^1/_4$	18.8	—	0.5	*0.4*	0.7	0.8	1.1	**1.4**	**1.4**	0.9	0.8	0.6	*0.5*	*0.5*	0.7	0.8	0.8	**1.4**	1.3	1.0							45
22	$1\,^1/_4$	18.8		2.0	2.2	**2.6**	2.4	1.5	1.1	*0.6*	1.0	1.1	1.5	2.0	2.3	2.4	2.4	**2.8**	2.4	2.0	1.4	*1.2*	1.4	2.6	2.6	2.7	2.7	60
36	$1\,^1/_4$	18.7	—	3.0	2.5	1.4	*1.1*	1.2	1.8	2.0	2.5	**2.9**	1.8	1.8	1.5	1.4	1.3	0.9	*0.7*	1.3	1.5	1.7	**2.3**	**2.4**	1.8	1.4	1.0	60
36	$1\,^1/_4$	18.8	—	2.2	**2.9**	2.4	2.5	2.4	2.2	*1.5*	1.8	2.2	2.4	**2.8**	2.7	2.6	2.4	2.0	*1.6*	1.8	2.1	2.3	2.7	**2.9**	2.2	1.9	1.8	45
10	$2\,^1/_2$	16.8	68	1.8	1.2	0.6	*0.2*	0.7	0.9	1.6	**1.8**	0.7	*0.5*	0.7	0.8	1.3	**1.5**	**1.5**	1.0	*0.5*	1.0	1.1	1.3	**1.7**	1.0	0.8	0.4	30—35
13	$2\,^1/_2$	17.0	69	2.0	*0.4*	**1.5**	1.1	1.0	1.0	*0.7*	0.9	1.1	**1.6**	1.4	0.8	1.4	**1.6**	0.9	0.8	*0.3*	0.5	0.9	1.1	1.3	**1.5**	1.2	0.9	30
22	$2\,^1/_2$	17.0	68	0.4	*0.3*	0.5	1.0	1.2	**1.5**	1.0	0.8	0.7	*0.3*	0.9	1.1	1.4	**1.6**	0.9	0.8	*0.3*	0.5	0.9	1.1	1.3	**1.5**	1.2	0.9	40
28	$2\,^1/_2$	17.0	69	1.2	1.6	**2.2**	1.2	1.0	0.7	0.5	*0.4*	1.0	1.4	2.0	**2.3**	2.0	2.0	1.6	1.0	0.9	*0.5*	*0.5*	0.8	1.2	1.7	**2.3**	1.5	45
45	$2\,^1/_2$	17.0	69	2.3	**2.5**	1.9	*1.5*	2.0	2.2	**2.3**	2.0	*1.3*	2.0	2.1	**2.4**	2.0	*1.6*	*1.6*	2.4	**2.5**	**2.5**	2.0	*1.6*	1.9	2.2	**2.4**	2.0	25

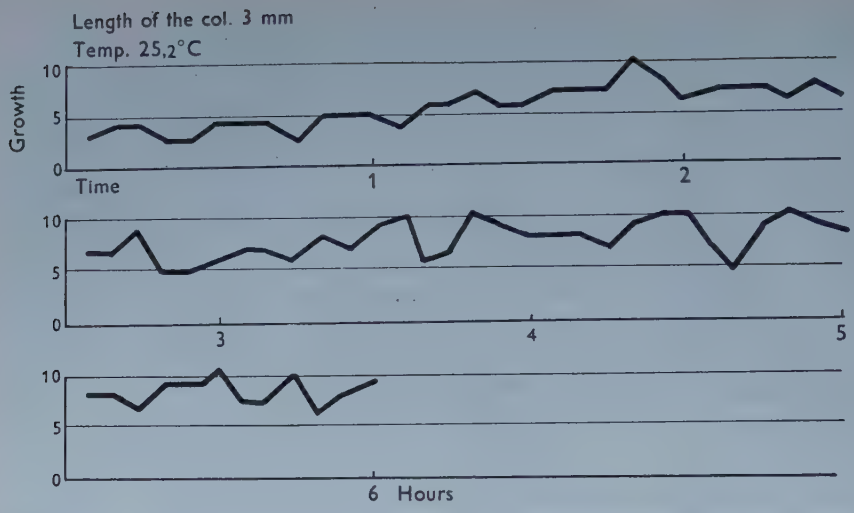

Fig. 4. Growth fluctuations in the coleoptile of the »Primus» oats (table X, col. A).

A certain irregularity of growth has previously been observed by several authors in vertically growing coleoptiles of *Avena* and descriptions of other kinds of periodical phenomena are to be found in literature (KARSTEN 1918, STÅLFELT 1927, *et al.*). As to the coleoptile growth, however, this has only been studied during short periods of time or with longer intervals of observation. In several series of experiments I have studied the growth during long periods and with readings performed at intervals of 5 min. The numbers of growth were stated in 1/10 dividing lines (= 8 μ). The course of the growth curves in two of these experiments is shown in figs. 4 and 5.

The growth is apparently not continuous. Its variation seems to be specially obvious in younger coleoptiles at a higher temperature. The regular undulatory course that could be recorded in table X (on the above preceding page) never finds expression, however.

The cause of this pendulous course of growth has been discussed by me (ERMAN 1933). Thus, it is possibly due to pulsation in the activation of the natural chemical growth factors or in their transportation.

BEYER (1927, 1928) could show that polarization phenomena play an important role in the transportation of hormones in plants, and BRAUNER (1927) found that the electromotive force arising on reorientation of different plant organs varies between 4 millivolts (for roots) and 9 millivolts (for grass internodes).

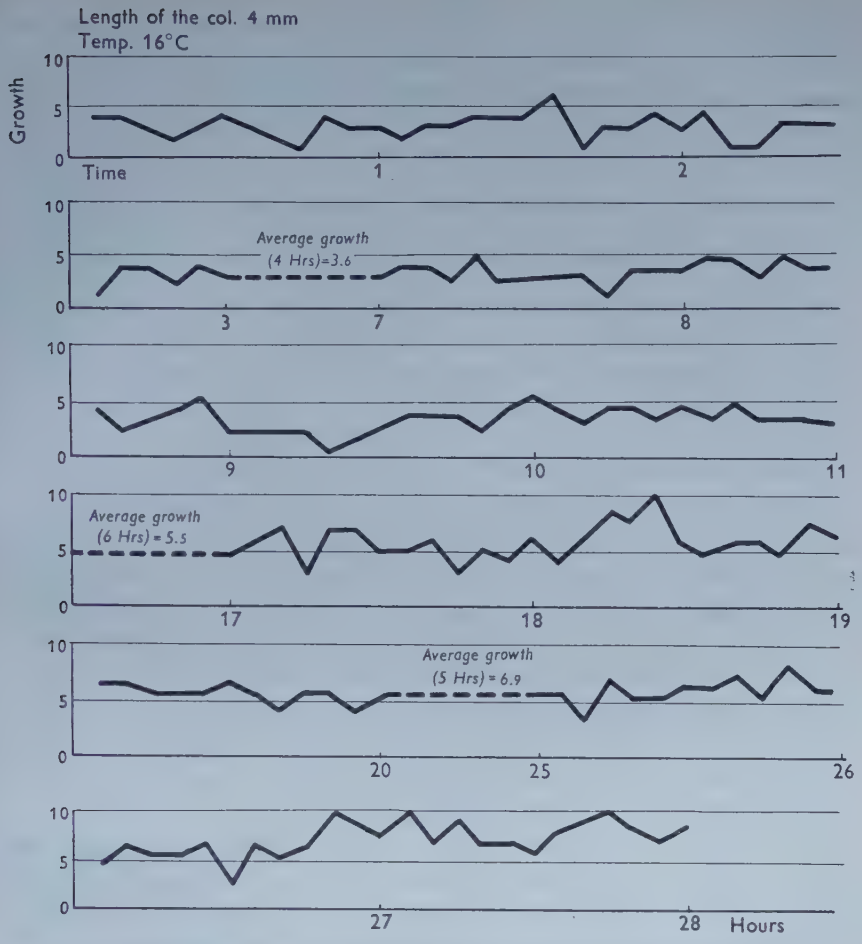

Fig. 5. Growth fluctuations in the coleoptile of the »Primus» oats (table X, col. B).

Van der Weij (1932, 1934) regards the intermicellar substance as the conveyor of the chemical growth factors, and Münch (1932) opines that a potential-fall from apex towards base may be considered the initiating factor, wherefore periodicity in the conductibility of the intermicellar substance — perhaps in its turn primarily occasioned by potential-oscillations — can give rise to these growth oscillations.

Cholodny (1927) also was of opinion that the distribution of the growth hormone in the plant is due to polarization phenomena, and that polarization first manifests itself in the appearance of an electropotential between different parts of it.

Table X. Growth fluctuations in the coleoptile of the »Primus» oats.

Coleoptile A. At the beginning of the experiment about 3 mm. Temp. 25.2° C.

3	4	4	3	3	4	4	4	3	5	5	5	4	6	6	7	6	6
		3.5						4.3						5.8			
7	7	7	10	8	6	7	7	7	6	7	6	7	7	9	5	5	6
		7.3						6.5						6.3			
7	7	6	8	7	9	10	6	7	10	9	8	8	8	7	9	10	10
		7.3						8.3						8.7			
7	5	9	10	9	8	8	8	7	9	9	10	8	8	10	6	8	9
		8.0						8.5						11.2			

Total 6 hours

Coleoptile B. Lenght of the col. about 4 mm. Temp. 16° C.

4	4	3	2	3	4	3	2	1	4	3	3	2	3	3	4	4	4
		3.3						2.7						3.3			
6	2	3	3	4	3	4	2	2	3	3	3	2	4	4	3	4	3
		3.5						2.8						3.3			

Average growth per 5 min. during 4 hours = 3.6

4	4	3	5	3	3	3	3	2	3	3	3	4	4	3	5	4	4
		3.7						2.8						4.0			
5	3	4	5	6	3	3	3	3	1	2	3	4	4	4	3	5	6
		4.3						2.5						4.5			
5	4	5	5	4	5	4	5	4	4	4	2	Average growth per 5 min.					
		4.7						3.8				during 6 hours = 5.5					
7	8	4	8	8	6	6	7	4	6	5	7	5	8	10	9	11	7
		6.8						5.8						8.2			
6	7	7	5	8	7	8	8	7	7	7	8	7	5	7	7	5	8
		6.7						7.3						6.5			
Average growth per 5 min. during 5 hours = 6.9						7	4	8	6	6	7	7	8	6	9	7	7
								6.3						7.3			
5	7	6	6	7	3	7	6	7	10	9	8	10	7	9	7	7	6
		5.7						7.8						7.8			
8	9	10	8	7	8												
		8.3															

Total 28 hours

Later on, Pohl (1936) could demonstrate that the chemical growth factors, on an artificial potential-fall, migrate to the positive pole. Consequently, if the endosperm in the *Avena* seed serves as the posi-

tive pole and the coleoptile as the negative one, this causes a decrease of growth in the latter, for according to Pohl the chemical growth factors reach the coleoptile from the endosperm in an inactive form. In this state they migrate apically and are activated in the apex of the coleoptile.

Katunskij (1936) found that coleoptiles with a positive pole placed on their base grow more quickly than normal. Is the anode, on the contrary, placed on the apex of the coleoptile, the growth falls below the normal. Clark (1937, 1938) could show that the coleoptile base in *Avena* and *Zea* is positive in relation to the apex, and that the zone with the strongest growth is always positive in relation to the other zones. In his experiments with roots, Lundegårdh (1942) found in their elongation zone a potential 20 to 30 volts higher than that in the posterior parts and in the apex. By this means auxin might be drawn from the apex to the zone of growth maximum but not past it. At horizontal position the potential-drop decreases on the upper side and increases on the under side while the auxin stream also decreases and increases respectively. The under side becomes positive in relation to the upper side.

Schrank (1944, 1948) who had subjected polarization phenomena in geotropic curvatures to detailed studies found that in a horizontally placed coleoptile the upper side was negative in relation to the under side. On that account he is inclined to make the transverse electric polarity responsible for the geotropic curvature and thus confirms the supposition of Borgström (1939) and other authors about a transverse transport of auxin being its cause.

Probably, then, electric potential-oscillations of longitudinal and transverse nature are finally responsible for variations in the transport of auxin or in the activation of growth factors and, consequently, for growth oscillations and nutations also. There is, however, reason to agree with Burström (1942) that the total metabolism as such is too much overlooked in the discussion of all these growth phenomena, while the hormonal aspect has been given too much precedence. Already Walter (1921) who studied growth oscillations in *Phycomyces nitens*, thus tries to explain these by presuming a connection between respiration, supply of material, and growth.

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ASYMBIOTIC GERMINATION OF ORCHIDS AND SOME EFFECTS OF VITAMINS ON THUNIA MARSHALLIANA.

BY

LARS ERIC HENRIKSSON.

A. Earlier investigations in asymbiotic germination and growth of orchids.

The orchid seeds are among the smallest and lightest of the phanerogams. The weight varies with different species from about 1.3 to 14 gamma, the length from about 0.15 to 2 mm (Burgeff, 1936). The testa may be ornamented in various ways and may form balloons or wings, which adapts the seed for distribution by air and water (Fig. 1). Inclosed in the testa lies the embryo, which may be composed of some hundreds of cells, though the number is often considerably smaller. An endosperm is lacking. The ripe orchid embryo in the capsula is free from the mycorrhizal fungus. In the ripe seed the lower suspensor cells are dead and empty, the basal cells being characterized by the great percentage of proteins and fat. For the rest the seed is rich in food reserves, especially fats. In uninfected, germinating embryos, the basal cells act as absorbing organs, while the suspensor cells provide the means of entry of the endophyte.

Bernard (1904, 1905) pointed out that orchid seeds could not germinate in aseptic cultures, but only after he had inoculated the cultures with his artificially cultivated, symbiotic fungus (*Rhizoctonia* spp.). In such cases, the natural symbiosis was produced. In 1909 Bernard modified his earlier statement, stating that though the embryos could undoubtedly develop on a sterile substratum, their development stopped at an early stage if the mycorrhizal fungus was not added. Bernard observed that the asymbiotic development

was favoured by more concentrated media, such media in his case containing, among other things, salep (the dried tubes of different species of orchids, used mainly as a drug) and saccharose. Burgeff (1909), who in the beginning was most interested in the endophyte, largely shared Bernard's later opinion as to the germination capacity of orchid seeds. Using an agar-medium containing 0.33 % saccharose and essential salts, the latter succeeded in germinating the embryos of *Cattleya* over a ten month period, during which time the seeds were kept in the dark. Afterwards the seedlings died, even thought hey were placed in the light.

As a result of his investigations into the influence of different carbohydrates upon higher, autotrophic plants, Knudson (1922, 1925) suggested that it was the task of the endophyte to furnish the orchid embryo with carbohydrate. He experimented with additions of pure sugars, as well as extracts of sugar containing substances, e.g. bog peat, carrot, garden beet, yeast etc. to a mineral agar solution. He found that a modified Pfeffer solution, when added with glucose or fructose, gave the best development in germinating terrestrial and epiphytic orchid seeds. Knudson (1924) proved that the development of the orchid seeds depends upon an external source of organic matter during the initial stages of germination. When the first leaves appear, the chlorophyll-bearing seedlings carry on photosynthesis themselves, and thereafter are able to grow on a non-organic medium. However, the development is more rapid if sugar is present. In this way Knudson (1930) induced a *Laelia-Cattleya* to bloom in asymbiotic culture.

Knudson (1925) verified that *Cattleya* embryos are able to use starch as a carbohydrate source after the cultures had been inoculated with the mycorrhizal fungus, *Rhizoctonia repens* Bernard. A 0.05 % glucose medium had the same effect as a 0.25 % starch medium inoculated with the mycorrhizal fungus. Following his results Knudson (1926, p. 1187) stated: ». . . germination with the fungus was due not to infection of the embryo but to the transformation of insoluble organic food in the culture medium to soluble foods and these with products excreted by the fungus were responsible for germination.»

Knudson (1922) showed fructose to be the best source of sugar in the case of *Laelia-Cattleya*. La Garde (1929), investigating the effect of different sugars on *Cattleya*, found maltose to be most favourable, a fact which was verified by Quednow (1930). Smith (1932)

used saccharose, maltose and glucose, but observed no difference. Wynd (1933 c) in an effort to determine the best source of carbohydrate for *Cattleya* obtained the best results with mannose, glucose, fructose, saccharose and raffinose, as listed in order of their effectiveness. Wynd proved that the pentose sugars could not support growth, and he also showed that the varying results of the effects of carbohydrates in the researches of his predecessors could be explained by the fact that they had used different mineral solutions. In this manner La Garde's result may be explained as due to the high concentration of mineral salts. Burgeff (1936), in *Vanda* experiments, obtained the best results with saccharose and glucose but found that maltose was useless. Burgeff expressed the opinion that use of glucose may be accompanied by disturbances in carbohydrate and protein metabolism. Schaffstein (1942) also found that saccharose was best in the case of *Vanda*.

Usually, pure glucose, saccharose or a mixture of glucose-fructose is used as a source of carbohydrate in asymbiotic orchid cultures, 2 % generally being added to the medium.

Knudson and his collaborators (Knudson, 1925) demonstrated that the hydrogen-ion concentration is of great importance in the germination of orchid seeds. *Cattleya* seeds were best able to utilize the carbohydrate in the medium at pH 4.6, at which value the germination was quite as good as if the mycorrhizal fungus had been present. The critical pH range for asymbiotic orchid cultures is between pH 4.5—5.5 (Knudson, 1925, 1946, La Garde, 1929, Burgeff, 1936 int. al.). At pH values above 6 the seedlings are chlorotic and die in a short time, while at pH values lower than 4.5 the growth of the seedling is inhibited, though chlorosis may not appear.

The nutrient medium generally used in asymbiotic germination of orchid seeds is weakly buffered (phosphates). This has obvious consequences, when one considers that the seedlings must be under sterile conditions for periods of from one half to two years before they may be transplanted to a natural medium in pots. To prevent too-great fluctuations in pH and to avoid effects produced by evaporation of the media, the seedlings are transplanted to fresh sterile agar every other month. Vacin & Went (1949 a) have stated in a preliminarily report that amino acids, which are excellent buffers, may be used in the germination of orchid seeds as well as in seedling growth.

Wynd (1933 a, b) studying the sensitivity of orchid seedlings to

nutritional ions, found that the best development occurred in media with a low concentration of phosphate. Burgeff (1909) established that in asymbiotic cultures the seedlings prefer ammonium salts to nitrates. Smith (1932) observed that in the case of Solution B (Knudson, 1922, 1925) a greater concentration of ammonium sulphate gave additional vigour to the plants. It is a fact that higher plants prefer ammonium salts to nitrates, if there is a good supply of carbohydrates.

Organic nitrogen requirements of the asymbiotic orchid seedling have also been studied. Holländer (1932) proved that orchid-fungus symbiosis involves a considerable contribution of organic nitrogen to the orchid. The concentration of nitrogen was 4.98 % in symbiotic *Cymbidium* seedlings, 1.66 % in asymbiotic ones, when the plants were grown on a sugar medium containing ammonium sulphate (Eg_1 solution, Burgeff, 1932). Burgeff (1936) tested the effects of 8 different organic sources of nitrogen, and found that only asparagin and nucleic acid (prepared from yeast) had the same positive effect as ammonium salts. Curtis (1947) was able to show that nucleic acid and peptone were most favourable for orchid seedlings and that the development was more regular. Spoerl (1948) examined the effects of 19 amino acids, and concluded that the very young *Cattleya* embryos preferred only arginine while the other amino acids inhibited germination. With older embryos, aspartic acid proved to be a good nitrogen source. Vacin & Went (1949 b) obtained better growth in tomato-juice-agar solutions than in a standard solution containing only mineral salts and sugar. The tomato-juice has a very good buffer action. Little or no pH change due to autoclaving resulted in those solutions having an initial pH of 3—6. Working with a *Cymbidium* hybrid, they added a protein hydrolysate, rich in amino acids and vitamins, to a pure inorganic medium; the resulting growth 150 days after planting was three times greater than in an ordinary medium containing inorganic salts and sugar. The hydrolysate stimulated growth only at concentrations of 1—2 %, higher concentrations being toxic.

It had earlier been thought that the importance of the mycorrhizal fungus lay in the fact that it supplied growth factors as well as carbohydrates to the orchid. Burgeff (1934) obtained a splendid development of *Vanda* when he added sterilized extract from pure cultures of the endophyte. Earlier it had always been difficult to culture the *Vanda* spp. on ordinary mineral salt sugar medium.

The same growth-stimulating effect was obtained by BURGEFF (1936) from different yeast extracts. His attempts to break off avitaminosis of the seedlings by using preparations of vitamin A, B_1, B_2, auxin, and follicle hormone, were a failure but he had positive results with vitamin »Harris», i.e. vitamin B_6.

SCHAFFSTEIN (1942) published a work on avitaminosis in orchid seedlings. He isolated a vitamin-like substance, vandophytin, from the mycelium of the mycorrhizal fungus. Greater quantities of vandophytin were isolated from seedlings of *Avena*, *Pisum* etc., from Acer leaves and pollen grains of *Pinus* and *Alnus*. Vandophytin is of common occurence in the plant kingdom, is thermostable and soluble in water and alcohol. 0.1 mg per liter of the purified preparation has an optimum effect on asymbiotic orchid seedlings. In the case of *Vanda*, however, an addition four times greater was needed in order to produce the optimum effect. The earlier negative results of pure vitamin effects were due to the fact that SCHAFFSTEIN only investigated the effects of nicotinic acid and nictotinamide in comparison with those of the vandophytin. A concentration of 0.2 mg per liter nicotinic acid produced an optimum effect, and the effect was twice as great as that obtained with the purest preparation of vandophytin. SCHAFFSTEIN's theory was that the avitaminosis indicated disturbance in the synthesis of carbohydrate due to lack of the respiratory coenzymes. When the young seedlings became rich in chlorophyll they were able to form the vitamin themselves. SCHAFFSTEIN conceived vandophytin as a derivative of nicotinic acid.

NOGGLE & WYND (1943) investigated the effects of vitamin B_1, B_2, B_6, C, nicotinic acid, and calcium pantothenate on the germination and growth of orchid seeds. In this connection they also studied the differences between maltose samples of varying degrees of purity. The seeds of a *Cattleya* hybrid germinated well on a mineral-salt-agar solution containing ordinary sugar, but did not germinate when purified maltose was used. This failure to germinate was not overcome by addition of vitamin B_1, C or calcium pantothenate. Vitamin B_2 caused poor germination and slow development; addition of vitamin B_6 resulted in good germination but later development was retarded. However, good germination and splendid development was produced by nicotinic acid in a concentration of 1 mg per liter, while a higher concentration of 10 mg per liter was less favourable. This vitamin was also found to stimulate the formation of aerial roots.

Since even purified sugars and ordinary agar may supply growth factors in the form of impurities, contradictory results may be obtained regarding the avitaminosis of orchid embryos and plants; such is the case of e.g. vitamin B_1.

The temperature factor may also be important. *Vanilla fragrans* germinated asymbiotically at a minimum temperature of 32° C according to investigation of KNUDSON (1950). The seeds of the hybrid *Vanilla fragrans* × *V. pomona* required 34° C. This, by the way, is the first time hybrid seedlings of *Vanilla* have been produced.

B. Experiments with Thunia Marshalliana.

In 1946 the author began an investigation into the effects of vitamins on asymbiotic germination of orchids. The material included *Thunia Marshalliana*, one hybrid of *Cattleya intermedia* × *Laelia anceps* and *Vanilla planifolia* ANDR. At present some pots of the *Cattleya* hybrid used in these experiments are in one of the greenhouses of the Botanical Garden in Uppsala. The experiments with *Vanilla* were unsuccessful since the author did not take into consideration the effect of temperature on this orchid (KNUDSON, 1950). To the author's knowledge, the experiments with *Thunia Marshalliana* are the first to be published.

Methods and culture conditions.

As a basic substratum Eg_1 (BURGEFF, 1932) was used in slightly modified form. The laevulose was excluded and the composition of the nutrient was as follows:

$Ca(NO_3)_2$ 4 H_2O	1.0	gm.
K_2HPO_4	0.25	gm.
KH_2PO_4	0.25	gm.
$MgSO_4$ 7 H_2O	0.25	gm.
$(NH_4)_2SO_4$	0.25	gm.
$Fe_3(PO_4)_2$	0.05	gm.
Glucose	10.	gm.
Agar	15.	gm.
Distilled water	1000.	ml.

The mineral-salts were pro analysis, the agar well washed in distilled water and the sugar of the highest quality obtainable from Pfanstiehl Chemical Co. The agar solution was autoclaved at 1.2 atm. pressure, and the pH after autoclaving was 4.9. The *Thunia*

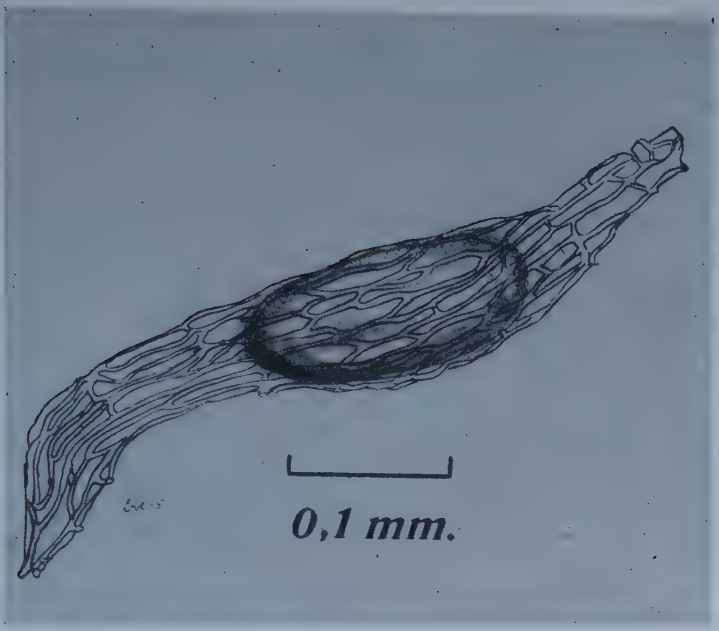

Fig. 1. Seed of *Thunia Marshalliana*, testa and embryo. — E. Henriksson del.

seeds, which are medium-sized orchid seeds (Fig. 1), were sterilized by the hypochlorite method of Wilson (Melin, 1939), the time of treatment being prolonged to ten minutes.

The seeds were then placed on slanted-agar tubes, each of which contained 10 ml. substratum. Every month the material was transplanted to freshly-prepared nutrient in order to avoid the effects of evaporation of the agar solution, as well as too-great fluctuations in pH. During the transplantations a thinning was made, so that at the end of the experiments each culture contained at most one or two plants (Fig. 2). After seven months 125 ml Erlenmeyer flasks (Pyrex) were used instead of test-tubes, each flask containing 25 ml nutrient solution.

The cultures were placed in a photothermostat with a constant temperature of 20° C. The illumination was produced by a common 500-watt bulb and a mercury vapour lamp, HgH 1000; the light being turned on for 10 hours each day. The average light intensity was 2000 lux. The cultures were repeatedly transposed so that each would receive the same amount of illumination.

The vitamins were added in amounts of 0.1 mg per liter (1 gamma

per tube). After 7 months, when the plants were transplanted to Erlenmeyer flasks, the amounts were increased to 0.2 mg per liter (5 gamma per flask). Vitamin C was added under sterile conditions after autoclaving, the other vitamins before.

All glassware was cleaned with chromic-sulphuric acid, rinsed several times with warm tap water, then filled with distilled water, and allowed to stand for least 24 hours.

Experiments and results.

The experiments were designed to show the effects of vitamin B_1, B_6, C and nicotinic acid, on the one hand individually and on the other hand in various combinations. The controls contained the complete nutrient solution without the vitamins. In figures and tables nicotinic acid is called p-p (pellagra-preventative vitamin).

Yeast extract was also used; but the concentrations employed were too high for satisfactory development (100 gm bakers yeast was dissolved in 500 ml destilled water. After 2 hours in a thermostat at 40° C, the solution was autoclaved, filtered and finally centrifuged. 1.0 ml yeast extract was then added to each tube).

After 14 days the seeds had swollen, the most advanced germination occurring in the vitamin B_6 cultures. In vitamin B_1 cultures the germination was also better than in the rest. (Table I.)

Table 1. Swelling and germination of *Thunia* seeds after 14 days, values given in relative amounts.

Control	Additions of vitamins							
	B_1	B_6	C	p–p	B_6p–p	B_1B_6C	B_6Cp–p	Yeast extract
+	+ +	+ + +	+	+	+	+	+	+

After 30 days the seedlings, by this time rich in chlorophyll, appeared green to yellowish-green while development was homogenous. Leaves and roots had been formed in all cultures after 150 days. The development was most advanced in those cultures containing only nicotinic acid, followed in succession by the controls and the cultures with only vitamin B_1. After 220 days, the total length was about 40 mm in the case of nicotinic acid, 15 mm with vitamin B_6, 30 mm with vitamin B_6 + nicotinic acid, 25 mm with vitamin B_1,

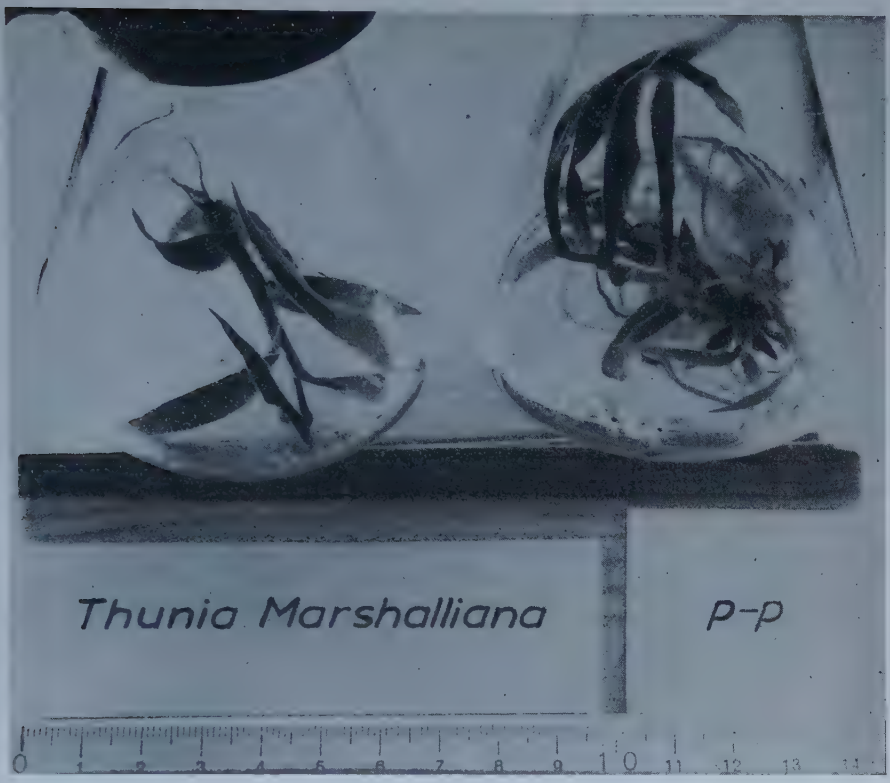

Fig. 2. *Thunia Marshalliana* plants, 308 days old, with addition of nicotinic acid.

and 22 mm with vitamin C. In the controls the length was about 25 mm. The yeast extract cultures had earlier become chlorotic and the development considerably reduced as a result.

After 308 days when the experiments were terminated, the largest plants occupied so great a portion of the Erlenmeyer flasks that sterile transplantation was no longer possible (Fig. 2). The plants were removed for examination and the dry weights determined. The data are given in Table II and Figure 3, some of the plants are shown in Figure 2 and in the Plates I and II.

The effect of the nicotinic acid alone was excellent, the best developed plants being in this series. The effect of vitamin B_1 was also good though it could not be compared with that of nicotinic acid. Vitamin B_6 favoured germination but had a retarding effect on the subsequent development. In the combination vitamin B_6 + nicotinic acid, the development was certainly better than that in

Table II. Effect of vitamins on *Thunia Marschalliana* after 308 days.

Series Additions	Dry weight in mg.	Max. no. of leaves	Length of the aerial parts i mm.	Max. leaf length in mm.	Max. leaf breadth in mm.	Max. root length in mm.
Control	30.8±0.9	5	48.0±5.0	42.0	5.5	60.5
B_1	59.1	6	83.5	65.0	8.5	92.0
B_6	18.1±0.7	6	48.0±8.7	25.0	4.5	58.5
C	30.1	6	55.5	42.0	5.0	55.5
p–p	86.6±5.6	8	101.0±4.0	73.5	9.0	176.5
B_6p–p	47.7±6.1	8	73.0±6.0	71.5	6.5	89.5
B_1B_6C	13.1±0.1	6	36.0±1.3	30.0	4.5	44.5
B_6Cp–p	40.5	8	84.0	71.5	6.5	78.5
Yeast extract	0.9	5	5.5	4.0	3.0	5.0

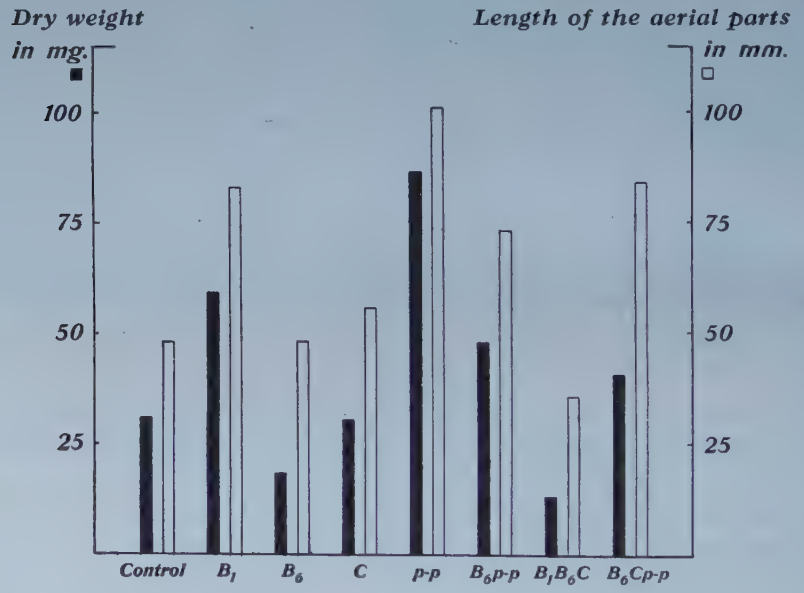

Fig. 3. Resulting growth 308 days after planting (*Thunia Marshalliana*).

the controls and in the series with vitamin B_6 but obviously poorer than with nicotinic acid alone. Obviously the favourable effect of nicotinic acid on the growth was counteracted during the later development by vitamin B_6. There seems to exist a similar antagonism between vitamin B_6 and vitamin B_1.

Undoubtedly, addition of vitamin C is unimportant in the asymbiotic germination of *Thunia* seeds.

In the combinations vitamin B_6 + nicotinic acid and vitamin B_6 + C + nicotinic acid there was excellent formation of root hairs in comparison with other series.

All plants were beautifully green, the controls showing only a slight indication of chlorosis at the leaf-tips.

Additions of nicotinic acid in quantities as small as 0.1—0.2 mg per liter are definitely growth-stimulative in the case of *Thunia Marshalliana*. The preceding investigators of asymbiotic germination and development of orchid seeds have generally used 1.0 mg of this vitamin per liter nutrient solution as a minimum addition (Noggle & Wynd, 1943, Bahme, 1949).

The experiments suggest that the young plants of *Thunia Marshalliana* are partially heterotrophic in regard to vitamin B_1 and nicotinic acid. However, it is interesting to note that each vitamin when used alone powerfully stimulates growth.

This seems to indicate that power to synthesize vitamin B_1 is increased in the *Thunia* plants provided that the available quantity of nicotinic acid is at an optimum; inversely, the synthesis of nicotinic acid is accelerated by an increased supply of vitamin B_1. The reason for the antagonistic effect of vitamin B_6 upon the effect of the above-mentioned vitamins must remain an open question for the present.

In the case of germination, both vitamins B_1 and B_6 have a stimulating effect but not nicotinic acid. It has been proved (Sherman, 1950) that a biochemical interrelationship exists between vitamin B_6 and fat metabolism, and it may well be that the effect of vitamin B_6 on the germination of *Thunia* seeds is associated with the high fat percentage of orchid seeds.

The Thunia Marshalliana plants were also analysed quantitatively for nitrogen by means of the titrimetric micro-Kjeldahl method (Hiller. Plazin & van Slyke, 1948). No obvious differences could be detected in comparison with the controls and the other plants. The mean value was 2.46 % total nitrogen of the dry weights. Problably the added vitamins do not cause any disturbance in nitrogen metabolism.

The author is greatly indebted to Mr. John F. Morgan-Jones, M. Sc., for revising the English of the manuscript.

Institute of Physiological Botany, University of Uppsala, June 1951.

Summary.

1. A short outline is given, reviewing previous investigations on asymbiotic germination in orchid seeds.
2. Thunia Marshalliana has been germinated asymbiotically for the first time, and the effects of vitamin B_1, B_6, C and nicotinic acid have been studied both separately and in various combinations.
3. Vitamins in concentrations of 0.1 mg and 0.2 mg per liter nutrient solution showed marked effect. Vitamin B_6 stimulated germination, but retarded the growth of the seedlings. Nicotinic acid greatly stimulated the development of the seedlings, their dry weights 308 days after planting being about three times greater then the controls.
4. The stimulative effect of nicotinic acid on the seedlings was partly reduced by vitamin B_6.
5. Vitamin B_1 stimulates later development but not to the same degree as nicotinic acid. No effect was shown in the case of vitamin C.

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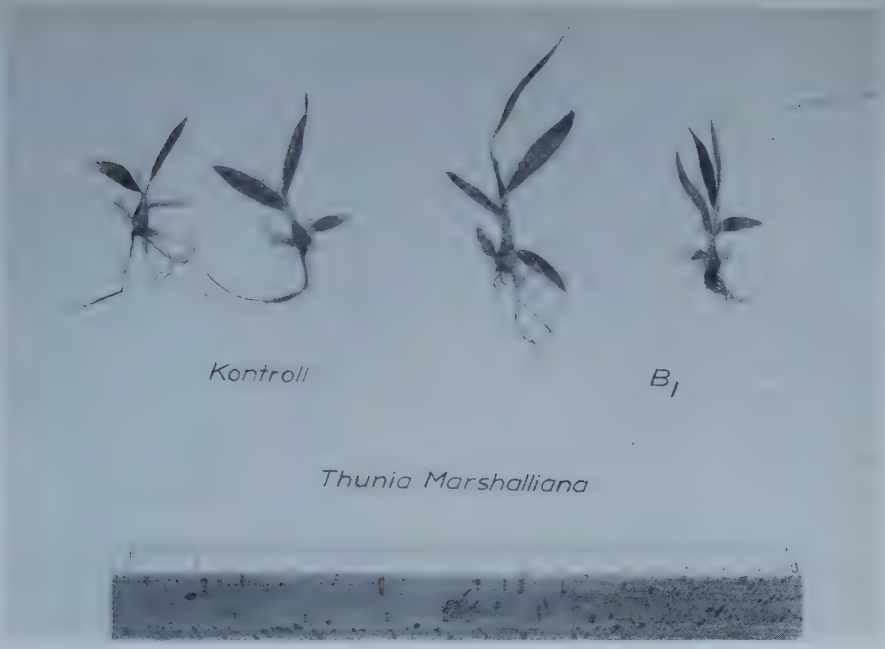
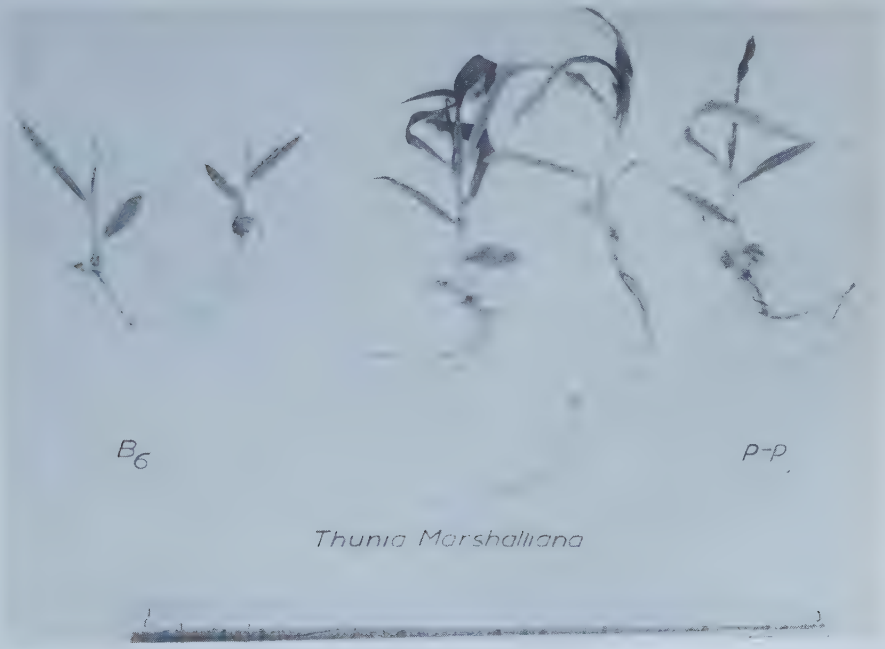

Kontroll
B1
Thunia Marshalliana

1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P-P
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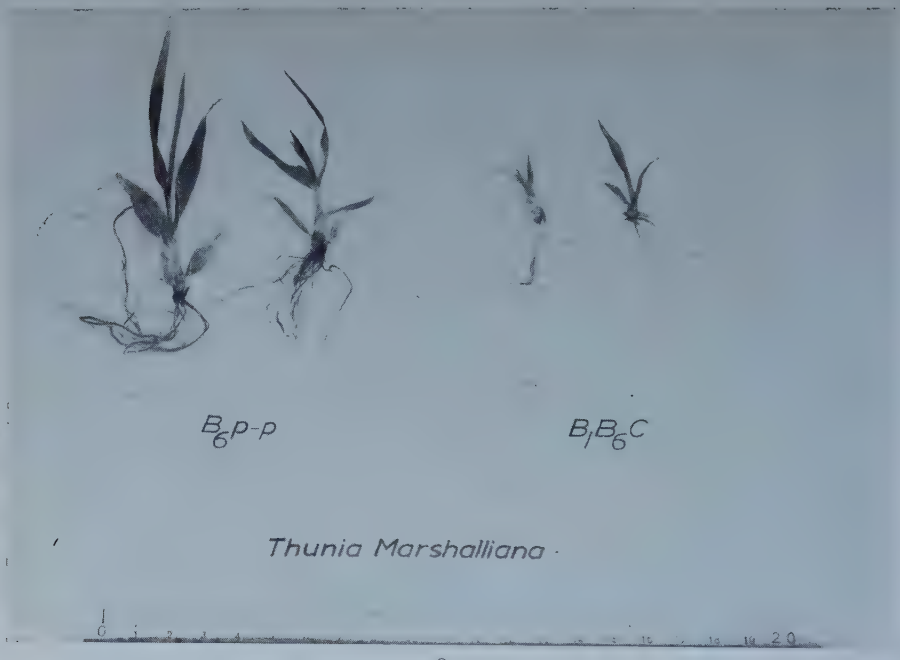
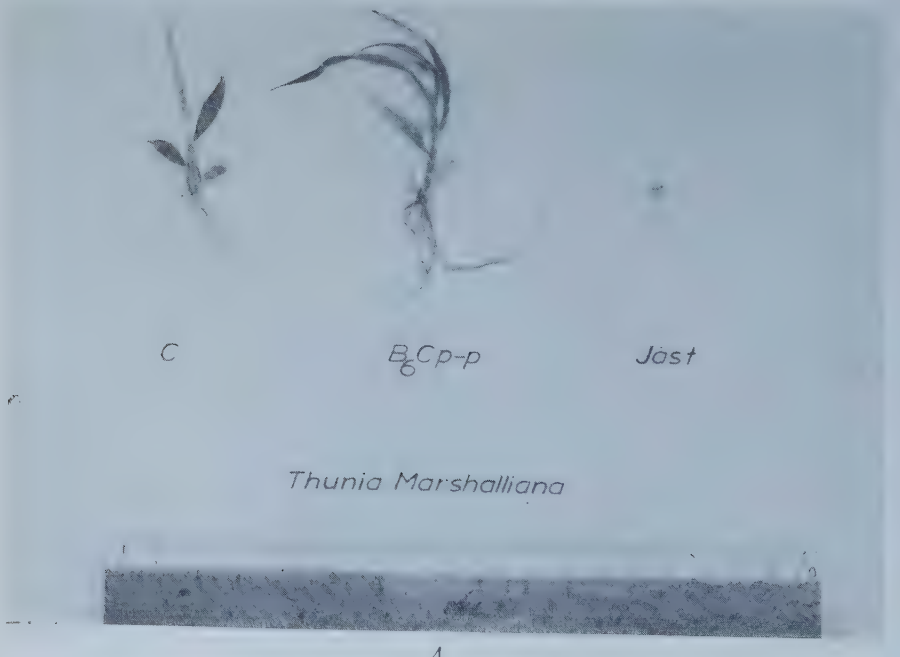
2


B_6p-p
B_1B_6C
Thunia Marshalliana

3


C
B_6Cp-p
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4

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Plate I and II. Effects of vitamins B_1, B_6, C, and nicotinic acid on growth of *Thunia Marshalliana* (308 days old).

Jäst = yeast; p—p = nicotinic acid.

Scale = 20 cm.

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THE CHLORATE METHOD AGAINST PERENNIAL WEEDS.

BY

ALFRED ÅSLANDER.

Chlorates h ave been used as herbicides for at least half a century. The earliest report of which the writer is aware dates back to 1901. Potassium chlorate was then tried on prickly pear i Australia, Anonymous (1901). The results seem to have been unsatisfactory. A considerable time elapsed before the chlorates are mentioned again, but around 1920 some experiments appear to have been started in France, Loyer (1923). Dilute solutions of ammonium chlorate were used for the eradication of annual weeds in grain crops. However, he also mentions that Rabaté recommends the application of 250 kg of sodium chlorate in a 2 per cent solution for the destruction of all vegetation on garden paths, etc., so that some experiments must have been performed earlier. In Norway, Korsmo (1925), in Denmark, Statens Forsøksvirksomhed (1925), and in Sweden, Feilitzen (1925), trials were reported on to ascertain the use of sodium chlorate for the eradication of weeds along ditches, roadsides, on tennis courts, etc., but no attempt appears to have been made up to that time to use chlorates against perennial weeds on arable land.

In 1925 the writer had the opportunity of starting some investigations on the eradication of perennial weeds, in the first place *Cirsium arvense* (L. Scop.), with suitable chemicals. Among the herbicides used, sodium chlorate was found to be the most suitable, Åslander (1926).

Basic investigations.

The eradication of perennial weeds must aim at the destruction of the perennial structures, the root or root system. That may be attained in two ways. The herbicide can be spread on top of the

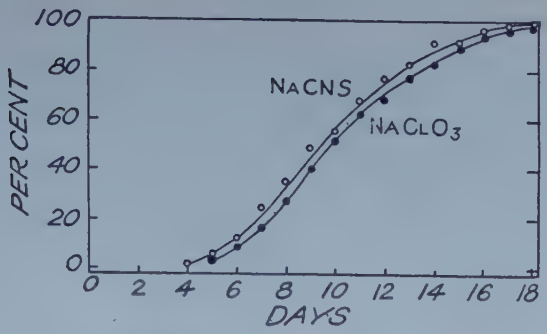

Fig. 1. Penetration of solutions of sodium thiocyanate and sodium chlorate through a silty clay loam. After 18 days the concentration of the solution leaching through a 15 cm column of soil was equal to the concentration of the solution added. (Åslander, 1928.)

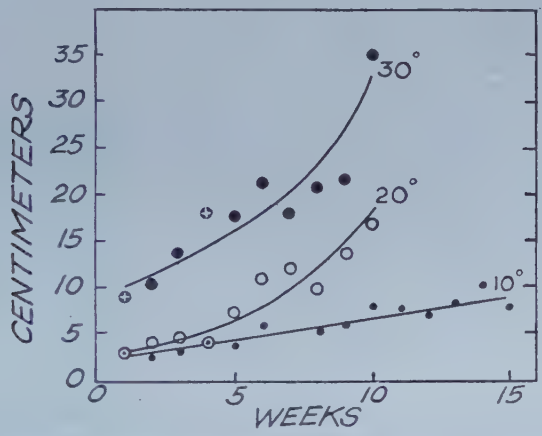

Fig. 2. Decomposition of sodium chlorate at 10°, 20°, and 30° C. Determined by height (cm) attained by barley seedlings when grown in soil to which was added 100 p.p.m. of sodium chlorate. (Åslander, 1928.)

vegetation with the expectation that it will penetrate from the leaves to the stem and further to the roots. As far as could be ascertained from the literature, this method made repetitions necessary, Stewart and Pittman (1924). The other method would be to apply the herbicide on top of the soil so that by the aid of surplus precipitation it penetrates the soil down to the roots. This would require a chemical that penetrates the soil freely. Further, the herbicide must decompose or leach out of the soil soon enough not to interfere with the normal crop production. Finally, the herbicide must be effective in relatively small quantities. Sodium chlorate was found to meet

these requirements, ÅSLANDER (1928). The penetration of sodium chlorate through a column of soil was found to be fairly rapid, Fig. 1. The rate of decomposition of chlorate in the soil was found to be dependent on the temperature, Fig. 2. In order to prevent too rapid a decomposition, sodium chlorate was applied towards the end of the growing season, when the soil temperature is comparatively low. An application of 200 kg of sodium chlorate per hectare late in the autumn was found to kill *Cirsium arvense* during the winter. Oats sown on the plots in spring grew as well as or better on treated than on untreated plots. Obviously, by the spring the chlorate had disappeared, most of it probably by leaching. A method was thus worked out for the eradication of *Cirsium arvense* without any interference with a normal crop production, ÅSLANDER (1928).

Field trials.

In 1941 it became possible to start field trials. Up to date, a total of 196 have been laid out. The influence of climate, soil type, time of distribution and the amount necessary for the eradication of various weeds was to be ascertained. The experimental fields were located in various parts of the country, mostly between 55° to 60° N. lat., but some up to 65° N. lat. Along the west coast the annual precipitation is relatively high, up to 1000 millimetres, while along the east coast amounts of 500 to 600 millimetres are common. The precipitation was recorded at each experimental field, as was also the soil temperature at a depth of 20 centimetres. The soil types varied from heavy clays to light sand and to humus soils. The time of treatment was extented from the earliest possible date after harvest until late in the autumn, especially in the southernmost districts, where the soil generally remains unfrozen until the end of December and sometimes does not freeze at all during the winter. The amounts spread generally varied between 100 and 200 kg per hectare, but in some cases larger quantities were applied. Lack of space prevents a complete report being given on the results obtained. Only some representative data have been selected.

In 1944—1945 a field trial was carried out at the Styrdal estate, *Gullbrandstorp*, on the west coast. The soil was a medium loam, well drained. The predominant weed was *Cirsium arvense*. Sodium chlorate was spread as dry salt at rates varying from 0 to 200 kg per hectare on three successive dates, *viz.* September 20, October 16,

and November 7. The plots were 50 m² and ran in triplicate. The following spring mixed grain of barley and oats was sown on April 12 and harvested on August 22. The trial was inspected on August 7 and the surviving weeds were counted on the plots on September 11. The main results are shown in Table I.

Table I. Relative yields of grain (barley and oats) and relative number of surviving weeds after treatment with sodium chlorate.

Date of treatment	Soil temp. °C.	Precipitation mm	Amounts of chlorate, kg per hectare			
			0	100	150	200
			Grain			
September 20	14	280[1]	*100*	115	119	125
October 16	11	187	*100*	123	119	129
November 7	4	131	*100*	123	110	128
			Number of shoots of *Cirsium*			
September 20	14	280	*100*	35	25	3
October 16	11	187	*100*	40	36	14
November 7	4	131	*100*	75	59	30

[1] From date of treatment until the soil froze.

The results summarized in Table I make it clear that an application of 200 kg of sodium chlorate did not harm the succeeding crop even when the treatment took place as late in the season as November 7. The precipitation in the district is fairly high so that the leaching of the chlorate is facilitated. The increase in the yields of grain is due to the fact that the roots of *Cirsium* act as green manure. The best effect of the chlorate on *Cirsium* was clearly obtained after the earliest application, which is probably due to the higher temperature, 14° C, as compared with 4° C at the time of the latest treatment. The fact that a few shoots were found even after the earliest treatment with 200 kg per hectare is taken as an indication of the difficulty of making a uniform distribution of the chlorate on a plot.

The trial analysed in Table I was carried out under somewhat favourable conditions: an extended season, fairly good precipitation, and a medium light soil. In most parts of the country the conditions are less favourable. The season is shorter, the precipitation less and the soil heavier. However, these conditions have been found not to exclude the possibility of success with the chlorate method.

Fig. 3. A. Untreated plot with spring wheat and *Cirsium arvense*. B. Plot treated with 200 kg of sodium chlorate per hectare in the autumn of the previous year by the original method. *Cirsium arvense* has been killed during the winter; the action on the spring wheat was favourable.

A typical trial was laid out at the Kättsta estate, *Skultuna* in 1944. The soil chosen was a medium clay, well drained. The predominant weed was *Cirsium arvense*, but in some parts of the experimental field clusters of *Tussilago farfara* were growing luxuriantly. Sodium chlorate was broadcast on September 21, October 13, and November 2. The plots were in duplicate only. The following spring the field was sown with oats on May 5 and harvested on September 9. It was

Table II. Relative yields of grain of oats and relative number of surviving weeds after treatment with sodium chlorate.

Date of treatment	Soil temp. °C.	Precipitation mm	Amounts of chlorate, kg per hectare			
			0	100	150	200
			Grain			
September 21	10	166[1]	*100*	103	113	115
October 13	8	118	*100*	104	97	100
November 2	5	80	*100*	102	96	90
			Number of shoots of *Cirsium*			
September 21	10	166	*100*	20	3	1
October 13	8	118	*100*	25	5	5
November 2	5	80	*100*	62	71	43

[1] From date of treatment until the soil froze.

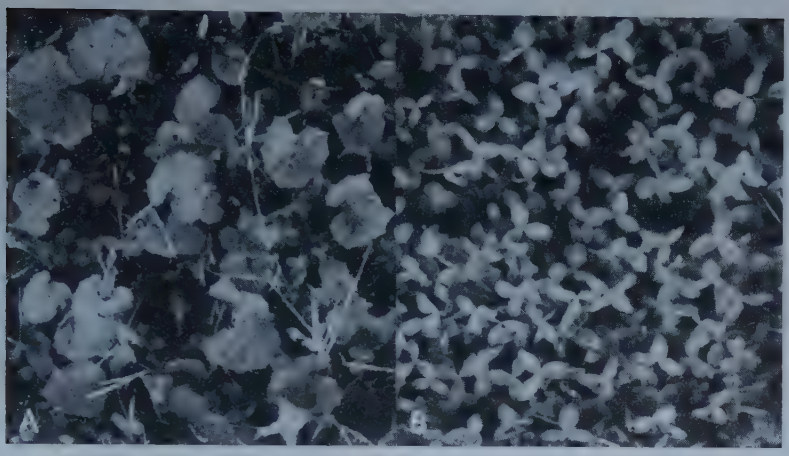

Fig. 4. A. Untreated plot covered with *Tussilago farfara*. B. Plot treated with 200 kg of sodium chlorate per hectare in the autumn of the preceding year. The photos were taken some time after the harvest of the grain crop, when the seedlings of red clover were growing luxuriantly, especially on the treated plots.

inspected on August 17 and the remaining weeds counted on September 14. The results of the trial are shown in Table II.

The data in Table II indicate that the yields of oats increased after the chlorate treatment of September 21, were unaffected when the chlorate was spread on October 13, and showed a tendency to decrease after treatment as late as November 2. A precipitation of 80 millimetres between the time of treatment and the freezing of the soil was insufficient to wash the chlorate out of the soil. The first treatment was, however, benificial in all respects. The oats thrived and the weeds were eradicated, also the *Tussilago*.

The new chlorate method.

Working hypothesis. So far the chlorate method was very effective against *Cirsium arvense* and *Tussilago farfara* when the chlorate was spread soon after harvest, or around the middle of September, and immediately ploughed under to a depth of about 20 cm. But some very common and very troublesome weeds such as *Sonchus arvensis* and *Agropyron repens* were unharmed, or practically so. It appeared highly desirable to work out a method that would kill *all* perennial weeds, but still without injury to the crop plants.

During the basic investigations it was found that sodium chlorate decomposes in the soil fairly rapidly when the soil temperature is high. For that reason it was supposed, in the first field trials, that the effect on the weeds would be more pronounced when the chlorate was spread while the soil temperature was comparative low, say around +10° C, than at a higher temperature. The results obtained were contrary to this assumption, the effect being clearly more destructive at a higher soil temperature, Tables I and II. This observation gave rise to the idea that *Sonchus* and *Agropyron* might be killed if the chlorate were applied at the highest soil temperature possible in the country, which is about +20° C. The poisonous action of the chlorate on the weeds would, of course, be accelerated at a higher temperature according to the general law of chemical reactions, but the important question was: would the chlorate penetrate the soil rapidly enough to kill the weeds before it became decomposed at the high soil temperature?

Experimental. The first trials on very small plots gave surprisingly good results, and thereafter common field trials were laid out. A typical trial of the first set was carried out at Valsäter farm, *Marma*, 70 km north of Uppsala on a humus soil with a subsoil of sand. *Agropyron repens* constituted about 50 per cent of the grass that had been cut two weeks earlier when the first treatment was given on July 18 and repeated on August 2 and 18. The field was

Table III. Relative yields of grain of oats and relative occurrence of *Agropyron repens* after treatment with sodium chlorate.

Date of treatment	Soil temp. °C.	Precipitation mm	Amounts of chlorate, kg per hectare				
			0	100	200	300	400
			Grain				
July 18	20	374[1]	*100*	140	148	139	155
August 2	18	243	*100*	108	119	110	111
August 18	16.5	123	*100*	11	134	117	127
			Agropyron in per cent of vegetation				
July 18	20	374	*100*	60	7	3	1
August 2	18	243	*100*	75	35	20	10
August 18	16.5	123	*100*	60	25	12	5

[1] From date of treatment until the soil froze.

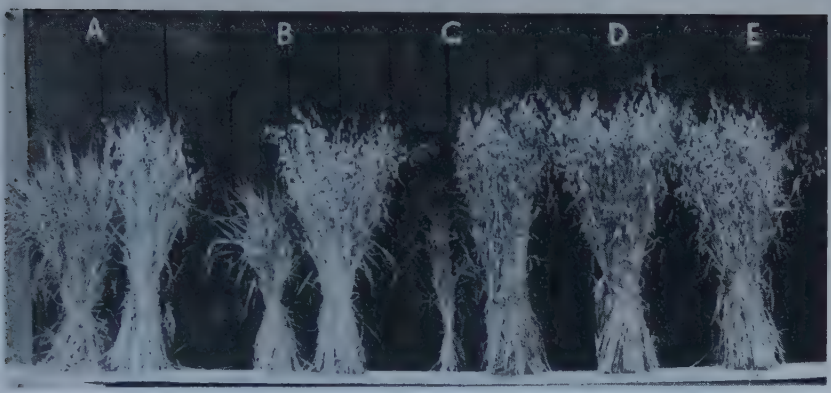

Fig. 5. Harvest of *Agropyron repens* and oats on one m². A. Untreated plot. B. 100 kg, C. 200 kg, D. 300 kg, and E. 400 kg of sodium chlorate per hectare spread according to the new method on July 18 of the preceding year. Compare Table 3.

ploughed on October 15. The following spring oats were sown on May 25 and harvested on September 2. The trial was inspected on July 12 and the effect on the weed was determined on September 27, when the *Agropyron* was growing luxuriantly on the untreated plot. The results of the trial are seen in Table III.

The data in Table III bring out the fact that large amounts of sodium chlorate were beneficial for the succeeding crop, especially when spread early in the season. The increase in grain shows that the rhizomes of *Agropyron* were quickly killed by the chlorate and thereafter decomposed. The second treatment did not give such good results as the third one, probably owing to heavy precipitation soon after the chlorate was spread. After the first treatment 200 kg of chlorate killed the *Agropyron*. The remaining 7 per cent of the number of weeds must be considered to have been an effect of an uneven distribution of the chlorate, Fig. 5.

Another trial was carried out at Husta farm, *Köping*, on medium clay, fairly well drained, also in grass. The weed flora was very mixed. Shoots of *Cirsium arvense*, *Sonchus arvensis*, *Achillea millefolium*, *Equisetum arvense*, and *Agropyron repens* were numerous. Chlorate was spread on July 19, August 3, and August 19 and the field ploughed on October 5. In the following spring mixed grain of barley and oats was sown on April 27 and harvested on August 8. The field was inspected on July 7 and the effect on the weeds determined on September 26. The data in Table IV give the main results of the trial.

Table IV. Relative yields of grain and relative effect on weeds after treatment with sodium chlorate.

Date of treatment	Soil temp. °C.	Precip-itation mm	Amounts of chlorate, kg per hectare				
			0	100	200	300	400
			Grain				
July 19	24.5	257	*100*	113	118	96	74
August 3	19	222	*100*	100	100	96	73
August 19	17	162	*100*	100	92	84	72
			Number of shoots of weeds				
	Cirsium		*100*	11	0	0	0
	Sonchus		*100*	16	0	0	0
July 19	*Achillea*		*100*	10	0	0	0
	Agropyron		*100*	67	1	0	0
	Equisetum		*100*	9	0	0	0

The results in Table IV differ a great deal from the results in Table III. We have here a distinct influence exerted by the type of soil. The results in Table III were obtained on a loose sandy humus soil, where the chlorate was easily washed out, so that even large amounts did not harm the succeeding crop. In the latter case the soil was a compact clay only fairly well drained, as the presence of *Equisetum* indicates. As a result the chlorate was leached only slowly. It had plenty of time to kill the weeds — and where large amounts were used the succeeding crop was harmed. However, 200 kg of chlorate per hectare was clearly beneficial, and larger amounts are never used in practice. The effect on the weeds was very pronounced. A dose of 200 kg per hectare killed everything. In Table IV only the effect of the first treatment is recorded in order to save space. A diminishing effect of later treatments was noted.

The latest developments. One great difficulty in handling the field trial was how to distribute the chlorate evenly. No other method could be used than broadcasting the dry salt by hand. Consequently, the effects of an uneven distribution could sometimes be noted both on the weeds and on the crop. In order to improve the evenness of the distribution the chlorate was dissolved in water and the solution spread with a suitable garden-sprayer equipped with four nozzles. In some of the concluding trials a comparison was made between broadcasting the dry salt and spraying it, in the latter case

Fig. 6. Spraying a plot on grass stubble with a solution of sodium chlorate.

with or without a wetting-agent added. One such trial was carried out on the estate of the Hamra Agricultural School, *Tumba*, about 20 km south of Stockholm. The soil on the experimental field was a light clay containing some »gyttja». The subsoil had a layer of »paper-gyttja», rather impermeable to water. The chlorate was spread on July 20, 1948, on stubble where green forage hade been cut for silage. The soil temperature was then 21° C. The predominant weed was *Agropyron repens*. The field was ploughed on October 25. A precipitation of 128.5 millimeters was recorded from the date of treatment until the freezing of the soil. In the following spring wheat was sown on May 3 and harvested on August 25. The field was inspected on August 8, and the effect of the treatment on the weed was determined on October 25, when the *Agropyron* was growing abundantly on untreated plots. In Table V some data are given regarding the trial.

The data regarding the yields of grain in Table V should not be scrutinized too closely. The trial was run in duplicate plots only, and the soil was somewhat uneven in fertility. But it seems safe to state that no harmful effect on the wheat can be noted — which is remarkable. The drainage of the soil was far from satisfactory. In

Table V. Relative yields of grain of spring wheat and relative occurrence of *Agropyron repens* after treatment with sodium chlorate.

Chlorate, kg per hectare	Grain	Weed
0	*100*	*100*
50, solution	160	42
50, solution +	118	30
100, dry salt	124	25
100, solution	125	20
100, solution +	136	17
150, solution	115	5
150, solution +	122	2
200, dry salt	115	4
200, solution	100	1
200, solution +	133	0

+ = a wetting-agent added.

fact, the writer would never have recommended the use of chlorate on such a soil. The trial was carried out in order to test the chlorate method under unfavourable conditions.

The effect on the *Agropyron* demonstrated in Table V seems to be more representative. The stand of the weed was very uniform at the

Fig. 7. A. Untreated plot, mostly *Agropyron repens*. B. Plot sprayed with 150 kg sodium chlorate per hectare with a wetting agent added on August 9, 1949. Photos taken August 10, 1950. The *Agropyron* has been converted into green manure.

start of the experiment. It is clear that a spray of 50 kg of sodium chlorate per hectare will injure the *Agropyron* considerably, and 150 kg, especially when a wetting-agent is added, will completely eradicate the weed. A spray appears to be more effective than broadcasting the dry salt, which must be attributed partly to a more even distribution. But the fact that the addition of a wetting-agent will enhance the effect must indicate that the improved contact between spray and weed is also of importance.

Discussion.

The results obtained in the trials, of which a few typical ones have been described above, indicate strongly that there is such a wide margin between the killing action of sodium chlorate on the perennial weeds and the harmful action on the succeeding crop that a safe method of weed eradication can be recommended. It is also clear that *Cirsium arvense* and *Tussilago farfara* are much more susceptible to sodium chlorate than are *Sonchus arvensis* and *Agropyron repens*. The former weeds are easily killed when the chlorate is applied late in the season when the soil temperature is just above freezing point while the latter ones must be treated so early in the season that the soil temperature is near $+20^\circ$ C. In other words, the former weeds are easily killed during the winter rest period, while the latter ones are susceptible only in the growing season. This difference appears to throw some light on the nature of the chlorate action.

In an earlier investigation, Åslander (1931), it was shown that sodium chlorate will kill only that part of a propagation root of *Cirsium arvense* with which a chlorate solution is in absolute contact, Fig. 8. For instance, if chlorate is applied to the middle part of the root, only that part is killed (and also the green top) but not the upper part of the root or the lower part. Both of these parts will form vigorous shoots. Through the upper part of the root enough chlorate may be conveyed to kill the green top shoot without any harmful effect on the root itself. It was also shown that when chlorate attacks the root of *Cirsium* the first sign of injury is the appearance of small brown spots on the surface of the root. The cells of the epidermis are killed and thereafter the destruction gradually works its way through the entire root. No absorption of chlorate by the root hairs is necessary for the killing action. The middle portion of the propagation

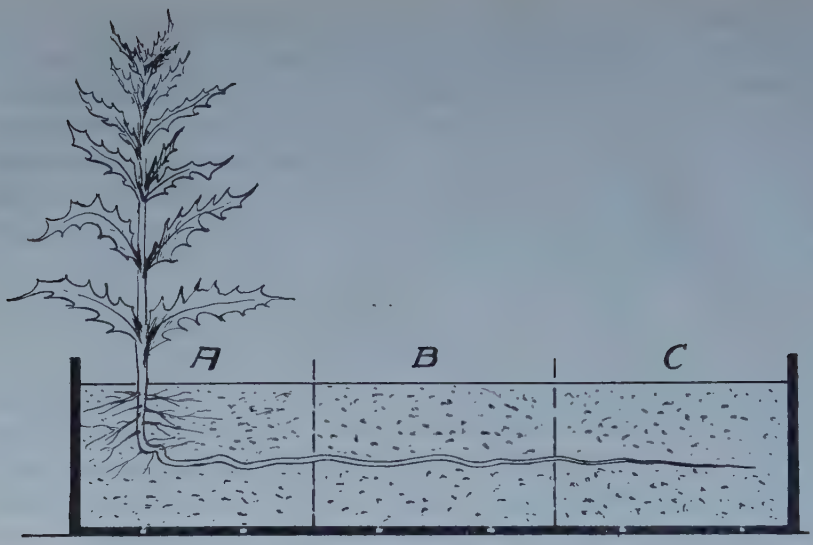

Fig. 8. Arrangement for studying the action of chlorate on *Cirsium arvense*. When a chlorate solution was spread on top of one of the sections, the part of the root in that section was killed (and also the green top), but outside the treated section the root was unharmed. There was indubitable a contact action.

roots of *Cirsium* very often has no absorbing roots, and the killing action may take place during the winter rest period. It is plainly a contact action that destroys the cells of the epidermis. Additional support to this theory of chlorate action is offered by the observation made in the trials that *Cirsium arvense* was more susceptible to the chlorate in heavy soils than in light soils. It was found that the epidermis of *Cirsium arvense* is of a far more sturdy structure on a root grown in a sandy soil than on a root taken from a heavy clay, Åslander (1931). Apparently the coarser structure developed in the light soil is an adaptation to meet the often low water content in such a soil.

From this point of view, that a sturdy structure of the epidermis offers good protection against the chlorate action, the failure of the chlorate to kill *Sonchus arvensis* and *Agropyron repens* during the winter rest period is easily explained. The epidermis of *Sonchus* consists of a layer of cork cells and the rhizomes of *Agropyron* are protected by a thick layer of lignified cells, Åslander (1931). However, the fact, that both *Sonchus* and *Agropyron* are easily killed by chlorate during the growing season indicates that the chlorate action is then caused by the absorption of chlorate and subsequent destruc-

tion of far more delicate structures than the epidermis. Åberg (1947) has studied the toxic action of chlorates upon young wheat plants grown in nutrient solution containing small amounts of chlorate. The investigation was thus a study of the injurious after-effects of an inappropriate use of chlorate for weed eradication on arable land. The main results lead to the conclusion that the chlorate ion lacks a general poisonous action upon living plasm. It is also suggested that the toxicity is due to a transformation of the chlorate in the sensitive cells, which is initiated by specific catalytic mechanisms, presumed to be the same as those which normally reduce nitrate. The last assumption is reached on the ground that the presence of nitrate in the nutrient solution diminished the chlorate action. In practical farming it has been known for several years that the yellowing of the seedlings of a crop after treatment with chlorate can be overcome by a top dressing of saltpetre. The writer, Åslander (1931), suggested that the toxic action of chlorate is a reduction to chloride producing nascent oxygen. Chlorates are very easily reduced by organic substances. Ekdahl (1947) suggests that the poisonous reduction substance is hypochloride.

The eradication of perennial weeds with moderate amounts of sodium chlorate is, however, only half of the chlorate method. An equally important part is the prevention of injury to the succeeding crop. When the method was worked out, Åslander (1928), it was ascertained that a chlorate solution easily penetrates a soil column and is easily washed out. It was also found that chlorate decomposes rather rapidly in the soil, especially at temperatures of +20° to +30° C. Such soil temperatures are, however, uncommon in nature. Only for a comparatively short time in the later part of July will the soil temperature rise towards or slightly above +20° C. Thus the decomposition of the chlorate in the soil becomes a factor of minor importance. The main factor is leaching when it comes to preventing an injurious effect on the succeeding crop.

The amount of precipitation necessary to leach out of the soil any injurious trace of chlorate depends on the type of soil and the method of chlorate application. Light soils, sand and loam, are more easily leached than clays, especially heavy clays. But still worse in this respect are humus soils, and among them especially »gyttja» soils, which very readily absorb water. According to the original chlorate method, the chlorate is spread on stubble, generally in September, and is immediately ploughed under to a depth of about 20 cm.

Leaching through the top soil is thus avoided. When the new chlorate method is used, the chlorate is spread on top of the soil, generally on grassland, in July or the beginning of August. The soil is ploughed late in the season after the chlorate has leached out of the top-soil layer. It would appear that the latter method is the more dangerous one for the succeeding crop because the chlorate has to be leached through the top-soil layer, the humus content of which will retard the leaching process. The trials have shown, however, that the new chlorate method is the safer one. The explanation is that the precipitation is normally abundant in July and August but decreases towards the autumn, (Table VI).

It has not been possible to determine with accuracy the minimum amount of precipitation necessary to make the chlorate method safe for the succeeding crop. The reason is that only a few of the — in all about 200 — trials have shown any harmful after-effects and in most of those cases a lack of precipitation was not the important factor. In the late summer and autumn of 1947 the precipitation was trifling. On many places the winter wheat sown in September did not germinate until November or not at all. Of the twenty trials with chlorate laid out that year only two showed any harmful after-effects on the crop in 1948, in both cases on humus soils. In one case only 42 millimetres of precipitation were measured between treat-

Table VI. Normal precipitation in various parts of Sweden during the season vital to the chlorate methods.

Place	Latitude North	Precipitation, m.m.					Date of freezing	Total precipitation	
		Aug.	Sept.	Oct.	Nov.	Dec.		I	II
Sunderbyn .	66°1′	58.4	50.9	48.1	40.6	29.0	X.23	85.8	146.2
Östersund ..	63°11′	77.9	47.8	42.3	32.2	33.5	XI. 1	90.1	169.0
Multrå	63°10′	75.0	47.0	38.0	33.0	29.0	XI. 5	91.0	166.0
Falun	60°37′	84.4	51.9	50.0	35.4	39.5	XI.11	97.7	199.3
Uppsala....	59°51′	75.8	50.4	50.5	41.3	45.4	XI.16	97.7	198.7
Örebro.....	59°16′	85.2	53.3	58.4	44.3	50.0	XI.21	116.4	228.3
Nyköping ..	58°45′	77.4	48.4	54.1	45.9	48.5	XI.27	118.3	219.9
Linköping ..	58°25′	67.6	43.4	50.3	40.5	39.3	XI.28	109.8	199.1
Skara	58°24′	84.2	54.2	61.3	44.3	41.4	XI.21	125.2	236.5
Kalmar	56°40′	59.8	46.5	37.6	43.4	40.2	XII.17	126.2	209.2
Halmstad ..	56°4′	109.7	68.6	69.1	62.4	71.5	XII.20	211.9	265.9
Lund	55°42′	76.5	50.3	57.5	58.6	54.8	XII.22	180.1	228.3

Fig. 9. A warning result of a faulty use of sodium chlorate. It has been spread too late in the season. In the background, an untreated area.

ment and the freezing of the soil. The injury was very severe. In the other case the recorded precipitation was 74 millimetres and the injury was slight. In Table II it is shown that a precipitation of 80 millimetres was insufficient to prevent injury on a medium clay soil. In Table VI are grouped together data regarding normal precipitation in millimetres per month during late summer and autumn at various places in Sweden and also the date when the mean temperature of day and night will reach the value of $\pm 0°$ C, Hamberg (1918), which is supposed to correspond to the freezing of the soil. In column I and II are added the amounts of precipitation from the proper time of chlorate treatment until the freezing of the soil. Column I corresponds to the original chlorate method and column II to the new method.

The data in Table VI indicate that the normal precipitation in Sweden north of Uppsala is on the borderline for the original chlorate method. The precipitation between the chlorate treatment and the freezing of the soil, Column I, is below 100 millimetres, but south of Uppsala the rainfall appears to be sufficient. For the new chlorate method, when the treatment takes place in late July or early August, the normal precipitation is more than sufficient throughout the country, Column II. The data in Table VI thus makes it clear that the limiting factor for the use of chlorate on arable land is not the precipitation. Everywhere the normal precipitation is sufficient to wash a normal amount of chloride out of the soil.

Fig. 10. A simple method of testing the after-effect of treatment with chlorate. Early in the spring samples of soil are collected on treated and untreated areas and planted with barley, which is very sensitive to chlorate. In the picture no harmful effect is noted.

The limiting factor for the chlorate method has been found to be the drainage of the soil. The drainage must *remove* the superfluous amounts of moisture, not merely store it in deeper layers. In several trials the drainage of the soil has been found to be insufficient. In some cases of light soils the natural drainage has been found adequate for normal crop production. The precipitation during autumn and winter is to a great extent stored in the soil but will not make the soil too wet in spring, and during the summer the water is used up by the plants. On such a soil the use of chlorate is dangerous. When a soil is drained the function of the drains is of the utmost importance. If the drains are placed too far apart, if the water table in the main drain is too high during the autumn, or the flow from the field is in any other way checked, then the chlorate will to some extent remain in the soil and injure the succeeding crop. On the other hand, injury has never been noticed in, for instance, heavy clay soils properly drained when the chlorate was spread early in the season and the precipitation was normal. Cases of severe injury have, however, occurred when the chlorate was spread so late in the season that the precipitation was very small before the soil froze. The precipitation in spring is generally low, so that leaching is then insignificant.

The perennial weeds may, in practical farming, be kept under

control by various means; complete eradication is more difficult to attain. An old method of value is summer fallow. The introduction of hormone derivates during the last few years aroused great expectations. An investigation of the use of 2.4-D, Åslander (1950), revealed the fact that the common weeds *Cirsium arvense* and *Sonchus arvensis* were easily checked by the hormone derivate, so that flowering and thus seed production were prevented but in the year following the treatment numerous shoots reappeared, especially when the treatment was followed by a period of somewhat low temperature. The use of 2.4-D on stubble in the autumn had no effect on the weeds in the following year. Moreover the commonly used hormone derivates are useless against *Agropyron repens*. The introduction a couple of years ago of the hormone derivate isopropylphenyl carbamate, active against grasses, does not seem to have found any practical application, Roland (1949).

For the complete eradication of the common perennial weeds summer fallow and the chlorate method may be said to be equally effective. That is to say, the summer fallow is effective only when attended to very carefully. By the ridgefallow method introduced by Korsmo (1930) and further worked out by the writer, Åslander (1937, 1945), a complete eradication of the perennial weeds is attained at a minimum of labour. The summer-fallow method is, nevertheless, very expensive as the eradication of the weeds must be bought at the prize of one crop. Compared with the labour and the cost of summer fallow the chlorate method is very convenient and inexpensive. Owing to the fact that even a small dose of chlorate will considerably weaken the stand of weeds, a combination of the chlorate method and summer fallow has been recommended. The writer (unpublished data) has found, however, that a dose of 100 kg of sodium chlorate per hectare in the autumn did not diminish the labour required to eradicate the weeds on the subsequent summer fallow. Vidme (1943) recommends that the chlorate treatment should be followed by a crop of potatoes or roots where the few remaining weeds can be easily eradicated by clean cultivation. The writer (unpublished data) found in a comprehensive field experiment that the chlorate treatment very markedly diminished the need of labour for clean cultivation in a field of sugar beet. The yield of beets was increased, as was also the sugar content.

The chlorate method against perennial weeds has been widely studied and used: Latshaw and Zahnley (1927) Rasmussen (1929),

Hulbert and Remsberg (1930), Hönningstad (1930), Yamasaki (1931), Muenscher (1932), Wexelsen (1932), Clouston and Hill (1933), Ling, and Haggard, (1933), Kieselbach, Petersen and Burr (1934), Tingey (1934), Crafts (1935 a, 1935 b, 1939 a, 1939 b), Rosenfels and Crafts (1941), Vidme (1943), Stålfelt (1945, 1946), Wiklander (1947), Schwanbom (1947), Åberg (1948), Domeij (1948), Ekdahl (1948).

However, considerations of space forbid a discussion on the results obtained as influenced by climate, type of soil and experimental conditions.

Summary.

1. A method for the eradication of perennial weeds on arable land with sodium chlorate without interfering with the normal crop production has been worked out and tested in about 200 field trials. The chlorate is spread on top of the soil, penetrates to the roots and kills the weeds. Next year a crop can be grown.

2. According to the original method 200 kg of sodium chlorate per hectare is spread on stubble preferably in August or early September and immediately ploughed under to a depth of about 20 cm. *Cirsium arvense* and *Tussilago farfara* will be killed during the winter rest period.

3. By the new method the chlorate is distributed at a soil temperature of up to +20° C in late summer on grass land or stubble and ploughed under in the late autumn. *Agropyron repens, Sonchus arvensis* and generally all perennial weeds are killed. When the chlorate is distributed by a spray with a wetting-agent added, a dose of 150 kg of sodium chlorate per hectare will kill *Agropyron*. The succeeding crop is harmed only under especially unsuitable conditions.

4. The action of the chlorate on *Cirsium* and *Tussilago* during the winter rest period has been found to cause the destruction of the delicate epidermal cells on the roots and rhizomes. It is a contact action. The roots of *Sonchus* and the rhizomes of *Agropyron* are protected by robust structures that will prevent the contact action of the chlorate during the winter rest period. When the chlorate is distributed at a high soil temperature it is absorbed by the roots, after which destruction sets in.

5. The chlorate treatment generally has a markedly beneficial influence on the succeeding crop. The competition of the weeds is

excluded and the root systems of the perennial weeds become decomposed and act as green manure. The rapid decomposition of the roots makes it clear that the bacterial activity of the soil is unharmed by the chlorate treatment. It was shown that the nitrification process in a soil is unaffected in spring after chlorate treatment in the autumn. Soil protozoa and earthworms were unaffected by the addition of sodium chlorate to the soil, Åslander (1928).

6. An inappropriate use of chlorate on arable land is dangerous for the succeeding crop. The chlorate must be removed from the soil before a crop can be grown. The removal is brought about partly by decomposition at higher soil temperatures, but mostly by leaching. A precipitation of 100—150 millimetres between the chlorate treatment and the freezing of the soil appears to be quite sufficient to remove injurious traces of the chlorate. The original chlorate method cannot be recommended where the season is short and the precipitation limited. The normal precipitation is, however, quite sufficient for the new chlorate method to be used anywhere in the country. The earlier in the season the chlorate is used, the less the danger of injurious after-effects.

7. The limiting factor of the chlorate method is the drainage of the soil. When the drainage system is well planned and working satisfactorily the proper use of chlorate is safe, even on heavy clay soils and humus soils, in which the percolation is restrained. The natural drainage, even of light soils, has often been found to be unsatisfactory.

8. The chlorate method is equally or even more effective against the weeds compared with summer fallow; the cost, however, is only about one-third. The use of 2.4-D in springsown grain crops has been found to prevent the flowering of *Cirsium arvense* and *Sonchus arvensis* and to some extent to reduce the number of shoots, while the yield of the grain crop generally decreased. A proper use of chlorate eradicates all perennial weeds and will generally cause a good increase in the yield of the succeeding crop.

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MACROPHYTE VEGETATION IN LAKES AND TEMPORARY POOLS OF THE ALVAR OF ÖLAND, SOUTH SWEDEN.

II. THE AQUATIC VEGETATION.

BY

HENNING HORN AF RANTZIEN.

The first part of this investigation was presented in a previous issue of this journal (pp. 72—120). Part II is devoted to a descriptive survey of the aquatic macrophyte communities. Besides, some characteristic alvar lakes and pools will be shortly described. — Advice and kind criticism have been received from Professor G. E. Du Rietz, Uppsala, and Mr. S. Olsen, Copenhagen. Furthermore, the writer is much indebted to Mr. R. Ross, London, who kindly read this paper in manuscript and revised it from a linguistic point of view.

Survey of the Aquatic Vegetation.

As has been stated in the general survey of the first part of this paper, the main vegetation zones of the alvar lakes are rather confluent. As a consequence, it is sometimes difficult to decide, whether a hydric plant community is properly to be placed in the amphibious or in the aquatic zone. In the present paper, the ecological classification is based upon the plants themselves, and not upon hydrographic lines. In conformity with this the basis on which the hydric plant communities are referred to the one zone or the other is the presence of those amphibious or aquatic components which are considered as differential indicator species of the zones.

The actual low-water line in summer is of little importance for the zonal classification. Changes are frequent and strong; in a couple

of hours the position of the water line may be very greatly altered, and in not very many more it may be back again at its former level.

During extremely dry and hot summers, many alvar lakes entirely dry out, except in the deepest parts. Drought catastrophes of that extent are not frequent, however. In such circumstances a number of aquatic plants will be killed. When a more normal water level has been attained again, colonization by obligate and facultative elodeids and facultative isoetids is comparatively rapid. The local distribution of the aquatic plant communities in the alvar lakes is closely correlated with these drought catastrophes, with ice erosion and with the kind and thickness of the sediments.

Almquist (1929, pp. 58—62) was among the first students of aquatic vegetation to emphasize that the sociological connection between aquatic plants is looser than the affinity observed in the amphibious or terrestrial vegetation. According to Almquist and others, the connection between plants of different layers is especially loose. Because of that, the interest has been focused on the study of one-layer communities, with the result that every layer is dealt with without any consideration of the other layers in the same piece of vegetation. This method, generally used in the study of Swedish lake vegetation, has been adopted in the present paper too, though the writer is aware that objections may be raised against the one-sided synusiological approach.

1. The aquatic reed-swamps.

In the alvar lakes, aquatic reed-swamps occupy only small areas. They are mostly to be found in the deep, central parts of the basins, often together with *Carex elata* swamps, and are characteristic of the more considerable deposits of lime gyttja. Only exceptionally are they dried out.

Dominants are *Carex lasiocarpa*, *Equisetum fluviatile*, *Menyanthes trifoliata*, *Phragmites communis*, *Scirpus lacustris*, *S. tabernaemontani*, and *Typha latifolia*. *Scirpus lacustris* and *Typha latifolia* have been observed each in one locality only (Möckelmossen and the alvar lake at Fröslunda, respectively). *Carex*, *Equisetum* and *Menyanthes* are generally to be found in comparatively shallow water. *Phragmites* and *Scirpus tabernaemontani* are the only really characteristic and frequent aquatic reed-swamp plants. In the alvar lakes, the helophyte layer may be combined with all other aquatic layers (only rarely with isoetids, however).

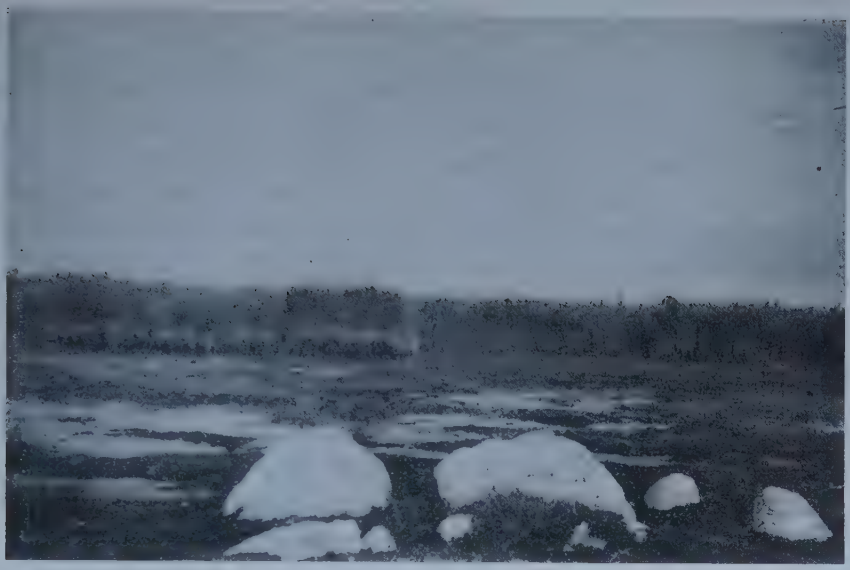

Fig. 1. Möckelmossen, eastern shore. In foreground *Scirpus palustris* - *Littorella* marsh with dominant *Littorella*, *Menyanthes*, and *Scorpidium scorpioides*. Waterholes with *Chara aspera*, *Scorpidium* and *Drepanocladus sendtneri*. In background aquatic reed-swamps with dominant *Phragmites communis*. July 20, 1949. Photo: the writer.

The aquatic alvar lake reed-swamps are not sharply differentiated from the amphibious ones. A number of amphibious components characteristic of the periodically submerged reedswamps, *e.g. Mentha arvensis* and *Galium palustre*, are not found in the aquatic ones; the latter are generally combined with obligate aquatic components from other layers (*e.g. Myriophyllum alterniflorum*), which do not occur living in any amphibious plant community. With respect to the aquatic reed-swamps it is doubtful, however, whether any helophyte is restricted to strictly aquatic conditions only; all or most of them are likely to be found in hydric amphibious associations also.

The differentiation into societies of this plant community of rather high rank is closely correlated with sediment and soil conditions (especially the varied content of organic matter), and furthermore with water depth, wind exposure, etc. These factor complexes have a considerable influence on the shoot density, too. Most aquatic reed-swamps of the alvar lakes are of the open, exposed type and do not reach the height and shoot density characteristic of those of sheltered localities. For the contrast between exposed and sheltered

reed-swamps see *e.g.* Du Rietz & Hannerz 1939, Stålberg 1939, and Thunmark 1931.

The aquatic reed-swamps are of comparatively little importance in the alvar lakes. The generally thin layers of soil and sediments, and the considerable ice erosion are probably responsible for this.

As the number of components is small, and societies formed exclusively by the dominant species prevail, no examples of the composition are given.

2. The aquatic nymphaeid vegetation.

The nymphaeid societies of the alvar lakes are small and fragmentary. Their slight development is probably a common feature to Swedish limestone lakes (see *e.g.* Almquist 1929 and Du Rietz & Hannerz 1939). The only dominant observed is *Potamogeton natans*. It occurs sparsely in the centre of the basins, generally at a depth of 40—60 cm. It is mainly found on loose calcareous mud (lime gyttja) comparatively rich in decaying organic matter. In the alvar lakes, at least in natural conditions, this species never attains the same density of floating leaves per m^2 as in the lakes of the Swedish mainland. The most luxuriant occurrence seen on the alvar was recorded from a small polluted pool to the south of Möckelmossen. The *Potamogeton natans* society may be combined with other layers (helophytes, elodeids).

Of other nymphaeids, the common dominants *Nuphar luteum* and *Nymphaea alba* are not found in the alvar lake vegetation. *Sparganium simplex*, which is rare here, sometimes occurs as a nymphaeid, but is mostly met with in its helophyte modification. *Potamogeton gramineus* is fairly common in the vegetation discussed but is only exceptionally found as a dominant. To some degree it holds an intermediate position between nymphaeids and elodeids.

3. The aquatic elodeid vegetation.

The elodeids constitute the most characteristic and most abundantly developed part of the aquatic vegetation in the alvar lakes. This layer is almost entirely dominated by one single species, *Chara aspera*. This has a rather wide ecological range (Sig. Olsen 1944, pp. 163—166). It grows luxuriantly in the alvar lakes and is represented by highgrown, coarse, rather spiny forms. The species

occurs in dense aquatic meadows in a varying depth of water (5—60 cm) and on all kinds of sediments, provided the sediment layer is sufficiently deep to let the rhizoids attach the plants to the bottom. The *Chara aspera* societies are vigorous on those parts of the bottom which are regularly subject to ice erosion (cf. the corresponding distribution in brackish water, Sig. Olsen 1945, p. 127, Luther 1951, p. 342); in the deeper parts, they are open and scarcer, and are often replaced by aquatic reed-swamps or patches of *Potamogeton natans* society. The preference of *Chara aspera* for the erosion zone may be explained primarily by its light requirements, which also have a bearing on its slight competitive power as compared with that of the reed-swamps and nymphaeid societies. In the alvar lakes, the result is to some extent an alternating local distribution of reed-swamps and *Chara aspera* societies, where the former are mostly found in localities not subjected to strong ice erosion or sheltered from ice pressure by local topographical features (rock fissures, moraine walls, etc.), while the latter are extensively distributed over the level limestone bottoms in shallow water.

Chara aspera is also the dominant species in the spring aspect of the amphibious vegetation zone. Sometimes an autumn aspect of *Chara aspera* is developed too. During these periods of the year, the lower (often also the middle) amphibious zone is regularly flooded for a sufficiently long time to allow an abundant vegetation of this species to develop. A *Chara aspera* aspect is usually found in the amphibious *Scirpus palustris - Littorella* marshes and in the hydric types of the amphibious *Agrostis stolonifera* heath. In the summer aspect of these plant communities the soil and bottom-layer are covered with a crust of dead whitish *Chara* which is sometimes rather compact. *Chara aspera* is sensitive to changes in the water level, and cannot survive more than a few hours if exposed to the air.

Whilst the island of Öland, outside the alvar proper, is characterized by a rich *Chara* flora, with most Swedish species represented, the *Chara* vegetation of the shallow alvar lakes and alvar pools contains remarkably few species. In addition to the polymorphic and luxuriant *Chara aspera*, which is one of the commonest alvar plants, only a few other species have been recorded during the present investigation, *viz. C. contraria*, *C. hispida*, and *C. vulgaris* ssp. *eu-vulgaris*. They have never been found as plentifully as *Chara aspera*, and their few localities on the alvar are all characterized by some

degree of pollution. Although additional species will no doubt be found, they are likely to be of importance only locally.

In the *Chara aspera* societies a number of other elodeids occur fairly constantly. These species (*Apium inundatum*, *Myriophyllum alterniflorum*, *Potamogeton filiformis*, *P. gramineus*, *P. pectinatus*, and *Ranunculus trichophyllus*) are generally not found as dominants, but they are of special diagnostic value for the elodeid vegetation and for the vegetation of the alvar lakes as a whole. From a trophic point of view this characteristic elodeid society is of great interest on account of its heterogeneous composition (Albertson 1950). It is necessary to point out that *Apium inundatum*, *Potamogeton filiformis* and *P. pectinatus* have been found only very locally in the alvar lakes (Sterner 1926, 1938, 1948).

The *Chara aspera* - *Myriophyllum alterniflorum* community described here is the characteristic elodeid vegetation for limestone lakes in Öland, Gotland and in parts of the Swedish mainland (see *e.g.* Almquist 1929, Ljungqvist 1914, Sterner 1926).

Of the analyses taken in the elodeid-layer of the alvar lakes, only the summary of 10 squares (each of the size of 1 m^2) from open water in the western part of Lake Möckelmossen needs to be recorded. Depth of water: 40—50 cm; depth of sediment (limnic chalk): 3—9 cm. July 19, 1949. — *Chara aspera* 3—5 (100), *Myriophyllum alterniflorum* 1—4 (60), *Potamogeton gramineus* 1—4 (50), *P. pectinatus* 2 (10). — For explanation of the figures, see Horn af Rantzien 1951, pp. 89—90.

4. The aquatic isoetid vegetation.

The isoetid societies of the alvar lakes are mainly to be found quite close below the low-water line, especially where a shallow depression in the bottom gives some protection from ice erosion. Those biotopes where lime gyttja has been accumulated to some degree are favoured. The isoetids are scarce or absent from the deepest parts of the bottom.

In the alvar lakes, the isoetid vegetation is almost entirely dominated by *Littorella uniflora*. Together with it *Echinodorus ranunculoides* is fairly constantly to be found. The latter has been observed as a dominant in small patches but it is more frequently met with as such in the amphibious vegetation. This isoetid two-species community is often found together with an elodeid society, the most important constituent of which is *Chara aspera*.

This isoetid community is allied to the amphibious *Scirpus palustris* - *Littorella* marsh. *Littorella* and *Echinodorus* are both found in the latter association. The aquatic isoetid society is distinguished, however, by being often combined with obligate aquatic plants from other layers (*e.g. Myriophyllum alterniflorum*) and by the absence of a number of amphibious components (*e.g. Mentha arvensis*) characteristic of the marsh vegetation.

Aquatic isoetid societies are especially characteristic of oligotrophic lakes. They are well developed in lakes of the Swedish upland, where they are formed by *Isoëtes echinosporum, I. lacustre, Littorella uniflora, Lobelia dortmanna, Ranunculus flammula* ssp. *reptans* and *Subularia aquatica* (Blomgren & Naumann 1925, Thunmark 1931, Lillieroth 1938, 1950).

Typical Examples on Alvar Lakes and Alvar Pools.

The present paper is based on field-notes from a number of lakes and pools in the southern alvar of Öland. All the localities examined have not been investigated completely. In several cases only a special type of vegetation was studied.

Seven alvar lakes and pools have been chosen out of the material and are described below. Their vegetation has been studied in detail. Nos. 1—2 are fairly typical, small alvar pools of the common »vät» type, temporarily water-filled. This type of pool is comparatively common throughout the alvar. The two examples have been chosen more or less at random. Nos. 3—5 represent three different types of alvar lakes. They normally retain some water also during extremely dry summers. Möckelmossen (No. 3), is the largest and the best known of all the alvar lakes in several respects. It is also the most typical of the three. No. 4 represents a type which is more influenced by human activities; it forms in other respects a transition to the lakes of the Swedish mainland. The alvar lake at Ebbelunda (No. 5) also differs a great deal from the »typical» alvar lakes, as represented by Möckelmossen. It is partly drained, surrounded by soils poor in lime and exemplifies a rather poor type. Nos. 6—7, finally, illustrate small bodies of alvar water created or strongly modified by human agency. The first one is a small alvar pool, somewhat deeper than the average, but originally probably of the common »vät» type. Because of its permanent character it is used as a cattle pool. The strong pollution of the water and the permanent

trampling of the shores have had several disturbing effects on the original vegetation. No. 7, a pool in a limestone quarry, was originally created by human agency.

1. Alvar of Resmo: Small (c. 200 m²) alvar depression c. 400 m E of the church of Resmo, c. 100 m N of the road Resmo—Stenåsa. Pool of temporary character, completely dried out in July—August 1949. The limestone rock is covered with thin layers of limnic chalk. — Vegetation: *Agrostis stolonifera* heaths of different types, replaced above by *Festuca-Tortella* heaths and, in some sections, by a *Sesleria-Ctenidium* meadow. — *Agrostis stolonifera*, *Alopecurus geniculatus*, and *Teucrium scordium* dominate in the field-layer of the central deepest parts (here *Veronica comosa*, *Inula britannica*, and *Plantago tenuiflora* are the most noteworthy components); *Drepanocladus aduncus*, *D. sendtneri*, and *Scorpidium turgescens* are the most important dominants in the bottom-layer. An *Agrostis stolonifera* - *Scorpidium turgescens* sociation and an *Alopecurus geniculatus* sociation without bottom-layer occupy the largest area in the center. All sociations are covered by a more or less compact crust of dead *Chara aspera* from the spring aspect. — In the marginal parts another type of *Agrostis* heath predominates, *viz.* a *Carex oederi* - *Drepanocladus sendtneri* sociation with *Potentilla anserina* and *Teucrium scordium* as subdominants in the field-layer.

2. Alvar of Resmo: Small (c. 500 m²) alvar depression c. 1000 m E of the church of Resmo, c. 150 m N of the road Resmo—Stenåsa. A pool of temporary character, completely dried out during July—August 1949. The limestone rock is covered with thin layers of limnic chalk. — Vegetation: entirely *Agrostis stolonifera* heaths of different types, replaced above by a *Sesleria-Ctenidium* meadow. The marginal parts are occupied by a *Carex panicea* consociation with *Scorpidium turgescens* and *Drepanocladus sendtneri* alternating in the bottom-layer. Subdominants in the field-layer are *Galium palustre* ssp. *eu-palustre* and *Mentha arvensis* f. *oelandica*. The *Carex panicea* consociation is replaced by an *Agrostis stolonifera* consociation in the central parts. Of the field-layer components, *Plantago tenuiflora* and *Veronica comosa* are especially notable; in the bottom-layer, *Drepanocladus sendtneri*, *D. aduncus*, and *Scorpidium turgescens* alternate as dominants.

3. Alvars of Resmo and Stenåsa (a small section in the extreme NW belongs to the alvar of Vickleby): Lake Möckelmossen, largest and most representative of the alvar lakes. The long axis of Möckelmossen runs N—S, at high-water the greatest length is about 2000 m and the greatest width c. 600 m, at extreme low-water the length may be reduced to 1/10 and the width to 1/3. The basin is even and shallow, with the greatest local depth c. 1.5 m. The sediments are lime gyttja and limnic chalk. The former is generally restricted to the central deep part, and to depressions in the marginal parts of the basin; limnic chalk predominates. The sediment

layers are usually thin (1—10 cm) and generally lie directly upon the limestone rock without any intervening soil layer; in the deeper parts, the lime gyttja has been accumulated into a layer up to c. 75 cm deep. Residual layers of *Carex* peat are found in the central parts. Ice erosion is strong and of considerable importance in influencing the local distribution of the vegetation. Möckelmossen is a seepage lake and normally lacks a defined outlet. The tributaries are temporary and more or less diffuse. The water level is directly regulated by precipitation and evaporation. Sudden changes in the water level are frequent, and the amplitude of the changes in water volume great. Except for grazing, which is at times heavy on sections of the western shore, the lake is little influenced by human agency; its present status probably reflects natural conditions. Some analyses of important hydrochemical factors may be found in Part I, p. 81, Tab. I.

The vegetation is rich and varied. The central parts are occupied by a large quagmire area with amphibious *Carex elata* swamps (locally with a light shrub-layer of *Salix cinerea*) and amphibious reed-swamps (dominated by *Menyanthes trifoliata*, *Phragmites communis*, etc., unfrequently combined with a bottom-layer). This quagmire area is surrounded by aquatic reed-swamps (dominated by *Menyanthes trifoliata*, *Phragmites communis* and *Scirpus tabernaemontani*); locally, patches of *Potamogeton natans* society are also to be found. In the E and NE, the aquatic reed-swamps change directly into the amphibious (*Menyanthes*-) reed-swamps and *Scirpus palustris* - *Littorella* marshes of the shore; in the N, W, and S there are areas of open shallow water. These open water areas are partly occupied by elodeid vegetation (mainly societies of *Chara aspera*, with *Myriophyllum alterniflorum*, *Potamogeton gramineus*, *P. pectinatus*, etc. as significant components); in depressions near the shore, somewhat sheltered from the strong ice erosion, and especially south of the *Carex elata* swamp, isoetid societies are to be found, dominated by *Littorella uniflora*, with *Echinodorus ranunculoides* as a subdominant.

The amphibious vegetation on the shores varies rather in different parts of the lake. The north-eastern, northern, and western sectors are characterized by a poor and monotonous vegetation, mainly *Agrostis stolonifera* heaths. In the field-layer *Agrostis stolonifera* is by far the most important dominant, followed by *Carex oederi*, *C. panicea*, and *Potentilla anserina*. In the bottom-layer *Scorpidium turgescens* and *Drepanocladus sendtneri* are the most important species. Sociations without or with a fragmentarily developed bottom-layer are fairly common too. In the hydric types a crust of dead *Chara aspera* is often observed. Near the water-line, small areas are covered with *Scirpus palustris* - *Littorella* marsh, dominated by *Scirpus palustris*, *Menyanthes*, *Littorella* and *Scorpidium scorpioides*. In the shore sectors described the soil-layer is very thin; areas without any soil layer also occur, and these are devoid of any macrophyte vegetation except *Nostoc commune* and crustaceous lichens.

The rock on the eastern shore is overlain by a moraine wall. For that reason it is steeper than the other parts of the lake shore. Immediately above the water line there is a more or less narrow border zone of *Scirpus palustris* - *Littorella* marshes (dominated by *Littorella*, *Echinodorus* and

Fig. 2. Möckelmossen, view from the south-eastern shore over the lake towards NW. Foreground thin, stony soil with light *Agrostis stolonifera* heath or without macrophyte vegetation. Left *Scirpus palustris - Littorella* marsh, behind that open water area, in background aquatic reed-swamps. Right shore barricade with narrow strip of *Carex panicea* meadow, changing upwards into *Sesleria coerulea - Molinia coerulea* meadow with *Potentilla fruticosa*. July 16, 1949. Photo: the writer.

Scorpidium scorpioides), amphibious reed-swamps (with *Menyanthes* as the main field-layer dominant and with a fragmentary bottom-layer) or transitional communities between reed-swamps and marshes, difficult to classify. The upper part of the shore is mainly covered with *Agrostis* heath often with *Carex panicea*, *C. oederi* and *Drepanocladus sendtneri* as the principal dominants. Locally we find transitional types of the *Carex panicea* meadow and more or less poor types of the latter association, mainly with *C. panicea*, *C. hostiana* and a number of typical meadow plants in the field-layer, and *Calliergonella cuspidata*, *Drepanocladus intermedius*, *Scorpidium lycopodioides*, etc. as bottom-layer dominants. This zone is delimited upwards by *Sesleria-Ctenidium* meadows or transitions between the latter association and the *Carex panicea* meadow.

The southern shore sector of Lake Möckelmossen, finally, is rather different from the sectors described above. There are thicker layers of soil, and the vegetation has a richer and more varied composition. The vegetation forms a complex mosaic with *Scirpus palustris - Littorella* marshes in the wet parts and different types of *Carex panicea* meadow in the drier marginal sections. The latter association is also found as islands in the marshes. The *Agrostis stolonifera* heath is less important than on the other parts of the shore. The marshes, which are dominated by *Scirpus palustris*, *S. tabernaemontani*, *Equisetum fluviatile*, *Eriophorum angustifolium*, etc. (rarely by *Littorella*), have a more or less fragmentary bottom-layer with *Scorpidium scorpioides* as the essential component. They regularly possess a thick and

compact crust of dry *Chara aspera*. *Carex oederi* and *Juncus articulatus* are important subdominants in the field-layer. The *Carex panicea* meadow which is typically developed in this southern part of the lake, is composed of dominating *Carex fusca*, *C. hostiana* and *C. panicea* and quite a number of meadow plants. The bottom-layer of the *Carex* meadow contains a large number of species, the most important of which are *Calliergonella*, *Campylium polygamum* and *C. stellatum*, *Ctenidium molluscum*, *Drepanocladus sendtneri* and *D. intermedius*, *Scorpidium lycopodioides*, *S. scorpioides* and *S. turgescens*.

The vegetation of Möckelmossen has been surveyed by Sterner (1926, pp. 75—77, figs. 17—18). — See furthermore the present paper, Part I, figs. 1—5; Part II, figs. 1—2.

4. Alvar of Stenåsa: alvar lake at the village of Fröslunda, about 3000 m NW of the church of Stenåsa. The greatest length c. 1000 m, the greatest width c. 400 m. The basin is shallow and even, the greatest depth is c. 1 m. The southern and eastern shores are overlain by moraine deposits; because of that, they are more steep than the other parts of the shore. The principal sediments are lime gyttja and limnic chalk. The former sediment has a wider local distribution than in Möckelmossen, and, in the central parts, it has been accumulated in rather thick layers. The lake is considerably more influenced by human activities than Möckelmossen. This is due to its being situated quite near the village of Fröslunda. The water is polluted by large flights of gulls nesting there, by a considerable number of grazing cattle, and furthermore by small quantities of sewage from the farm houses. — Some analyses of important hydrochemical factors may be found in Part I, p. 81, Tab. I.

The vegetation is formed by the same associations as in Möckelmossen, but the local distribution and development is somewhat different. In the centre, there is a large *Carex elata* swamp, surrounded by aquatic reed-swamps which in density and height exceed those observed in Möckelmossen. Principal dominants are *Phragmites*, *Scirpus tabernaemontani* and *Typha latifolia*. In the marginal parts of the reed-swamps, *Menyanthes trifoliata* is the main dominant, and societies formed by it cover considerable areas. Open lagoons in the reed-swamp are occupied by elodeid and nymphaeid societies (dominated by *Chara aspera* and *Potamogeton natans* respectively). Between the reed-swamps and the shore there is a free and open water area without any helophyte vegetation forming a narrow strip along the eastern and southern shores, but growing broader along the western shore. In the open water there is an abundant elodeid vegetation (mainly a *Chara aspera* society) or isoetids (with dominant *Littorella*).

The amphibious vegetation of the eastern and southern shores differs rather from that in the west. In the eastern and southern sectors, the aquatic reed-swamps reach near to the shore. The amphibious vegetation is thus sheltered from strong winds, wave action and strong ice erosion. This shore is furthermore rather steep. At the low-water line there are amphibious reed-swamps dominated by *Menyanthes trifoliata*. They are differentiated only vaguely here from the aquatic reed-swamps but are fragmentary

and of not much importance. Above them or alternating with them we find a narrow strip of *Carex elata* swamp. The association is often luxuriantly developed; a bottom-layer is mostly lacking. Above this »Magnocaricion» vegetation there is a more or less narrow belt of »Parvocaricion» vegetation, partly belonging to the *Agrostis* heath, partly to the *Carex panicea* meadow. The two latter plant communities are not quite typically developed; the vegetation grows under conditions not characteristic of the alvar biotopes. In both cases *Carex fusca* and *C. oederi* are the most important dominants, and the principal differences between the associations lie in the bottom-layer. The amphibious zone is bounded above by a heavily grazed terrestrial meadow, which is not of alvar type. — It should be noted that the shore zonation observed: reed-swamps — *Carex elata* swamps — »Parvocaricion» vegetation, is not at all characteristic of the alvar lakes.

Large areas of the lower amphibious zone on the western shore are covered by typically developed *Scirpus palustris - Littorella* marshes with *Littorella uniflora* as the main dominant. Usually, there is a crust of dead *Chara aspera;* the bottom-layer — if present — is formed almost entirely of *Scorpidium scorpioides*. Important subdominants in the field-layer are *Glyceria fluitans*, *Juncus articulatus*, *Ranunculus flammula* ssp. *eu-flammula*, and *Scirpus palustris*. The bottom is flat, and the layers of soil and sediments are comparatively thin. In the middle and upper amphibious zone the *Scirpus palustris - Littorella* marsh is replaced by amphibious *Agrostis* heaths of different types. The most important dominants in the field-layer are *Carex fusca* and *Agrostis stolonifera*, while *Drepanocladus sendtneri* and *Scorpidium scorpioides* alternate as main dominants in the bottom-layer.

A photograph of this lake, taken at low water in summer, is to be found in Sterner's paper of 1948 (fig. 52, p. 150).

5. Alvar of Stenåsa: alvar lake at the farm of Ebbelunda, about 2000 m W of the church of Stenåsa; marked »Torvmossen» on the topographical maps. Originally the greatest length was about 2000 m, the greatest width about 600 m; owing to drainage operations the former lake basin is now a system of small lakes communicating at highwater. No defined tributaries of any importance are to be found. The basin is very shallow (probably not more than c. 0.5 m at normal low-water). The fluctuations of the water level are great. A small shelf, excavated by the waves, forms a definite shore line. The lake system is surrounded by soils and deposits poor in lime; as a consequence of that the vegetation is poorer than in the other lakes described. A number of vegetation types and components otherwise characteristic of the alvar lakes are of little importance, or more or less absent. Another notable difference is that comparatively thick layers of soil reach to the low water line. Thin soil areas, bare rocks and plant communities more or less bound to them are only locally important. Apart from the drainage operations, human influence is insignificant; in this respect the Ebbelunda lake is the least affected of the three alvar lakes described here. Some analyses of important hydrochemical factors may be found in Part I, p. 81, Tab. I.

The aquatic vegetation is poor. Reed-swamps, nymphaeid communities,

Fig. 3. Small, permanently water-filled alvar pool, 500 m SW of the southern end of Möckelmossen. Used as a cattle-pool; the shores (mostly *Agrostis* heath) heavily grazed and trampled. In water *Potamogeton natans* society and *Chara vulgaris* ssp. *eu-vulgaris* society. July 16, 1949. Photo: the writer.

and isoetid vegetation are of no importance or lacking. Large areas of the chalky bottom are devoid of any macrophyte vegetation; in other localities there are light mats of *Chara aspera;* they seldom reach the same luxuriant growth and development as *e.g.* in Möckelmossen.

Turning to the amphibious vegetation, there are wide areas covered by a rather impoverished type of *Scirpus palustris* - *Littorella* marsh. Several of the characteristic dominants of this association are absent or of no importance, *e.g. Echinodorus*, *Glyceria fluitans* and *Littorella*. The most important dominant is *Juncus bulbosus*. Together with it *Scirpus palustris*, *S. uniglumis*, *Juncus articulatus* and others occur as dominants. A bottom-layer is usually absent; if present it is dominated by *Scorpidium scorpioides*. Of the other field-layer components *Mentha aquatica*, *Menyanthes*, *Potamogeton gramineus*, *Ranunculus flammula* ssp. *eu-flammula*, *Scirpus tabernaemontani*, *Triglochin palustre*, *Veronica comosa*, and *V. scutellata* are the most notable ones. A *Chara aspera* crust is often developed, but it is not so thick or widespread as in the other alvar lakes. Where the limnic chalk is replaced by alvar soil, there is a *Carex panicea* meadow of a peculiar type. Though rather poor in species, it is characterized by some of the most significant indicator species of the amphibious meadow association in the field-layer (*Eriophorum latifolium*, *Parnassia*, *Pinguicula vulgaris*, *Potentilla erecta*, *Primula farinosa*, *Sesleria* and *Viola canina*). *Schoenus ferrugineus* is found here too, but very sparsely. The mesic types are dominated by *Carex hostiana*, the hydric sociations by *C. panicea*. Above, this *Carex* meadow changes into a fairly typical but poor *Sesleria-Molinia-Ctenidium* meadow.

6. Alvar of Resmo: small (size c. 200 m²) permanently water-filled alvar pool, c. 500 m SW of the southern end of Möckelmossen, immediately S of the road Resmo—Stenåsa. The basin is probably a natural alvar depression though the border is steeper than in the most alvar pools visited. There are comparatively deep sediment layers (c. 40 cm) consisting of lime gyttja. The greatest depth is c. 1 m. The pool and its surroundings are strongly influenced by heavy grazing. It is much used as a cattle pool on account of its permanent water supply. The amphibious vegetation is trampled into fragments; in the summer the water is strongly polluted; during July—August 1949, it had a strong vegetation colouration. — Some analyses of important hydrochemical factors may be found in Part I, p. 81, Tab. I. — The amphibious vegetation is mainly represented by a rather fragmentary *Agrostis stolonifera* sociation without any bottom-layer. This plant community is replaced above by a *Sesleria-Molinia-Ctenidium* meadow, likewise fragmentary. In the aquatic vegetation, a *Potamogeton natans* society and a *Chara vulgaris* ssp. *eu-vulgaris* society cover the greater part. In addition to these, only single individuals of *Echinodorus ranunculoides*, *Alisma plantago-aquatica*, and *Equisetum fluviatile* are to be found.

7. Alvar of Torslunda: small (size c. 100 m²) permanently water-filled pond in a limestone quarry on the alvar c. 1500 m SW of the village Ölands-Skogsby and E of the road Ölands-Skogsby—Vickleby—Resmo. The pond is entirely the result of recent quarrying. The border is steep. The water depth in July—August 1949 amounted 0.5—1.1 m. Variations in water content are probably comparatively small. The bottom is covered by waste products from the quarry; between the splinters and flags of limestone there are patches of lime gyttja. — Some analyses of important hydrochemical factors may be found in Part I, p. 81, Tab. I. — No amphibious vegetation is to be found. In addition to one single specimen of *Typha latifolia* and some few culms of *Alopecurus geniculatus*, the lime gyttja is covered by a dense *Chara contraria* society and a *Drepanocladus aduncus* society.

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Svensk Botanisk Tidskrift. Bd 45, H. 3. 1951.

EN NY SELIGERIA-ART FRÅN NORRA GRÖNLAND.

AV

W. R. UGGLA.

Bland den danska Peary Land expeditionens 1947—50 stora insamlingar befann sig en *Seligeria*-art, som dr Kjeld Holmen godhetsfullt översände till mig för bestämning.

Nämnda *Seligeria*-art insamlades av expeditionens geolog dr J. Troelsen den 1 okt. 1948 som nr 6466 vid nordkusten av Independence Fjord vid Graptolit Elv Lat. 82° 19′ N. Long. 24 1/2° W. Alt. 50 m.

Vid undersökningen av nämnda fynd fann jag, att här förelåg en ny *Seligeria*-art. Som framgår av nedanstående utdrag ur dr. Holmens brev till mig av den 17.4. 1951, var han inne på samma tankegång:

»Jeg sender Dem hermed en lille pröve af den omtalte art, som jeg mener må stå när *S. oelandica* eller *lapponica*, eller i det mindste tilhöre den av Dem opstillede gruppe *Macrosporia*, idet sporene på min art er 21—22 μ. Arten kunne på den anden side godt minde en del om *S. polaris* både hvad habitus og hörnceller angår, men den adskiller sig fra denne især på sporestörrelsen, på det dypt indsänkede peristom, og på det, at columella mangler i sporehusene, og derfor kan väre forsvundet sammen med låget, altså fastvokset til detta. Desvärre mangler låget på alle sporehusene i pröven, så dette har ikke kunnet studeres.

Såvidt jeg kan se er det hverken *S. oelandica* eller *S. lapponica*, men hvad er det da? Jeg håber, at de kan klare problemet.»

Seligeria groenlandica W. Uggla sp. n.

Monoica. Caespites atrofusci ad subnigros, leviter †ophacei. *Caulis* ad 25 m/m longus, ramosus. *Folia* caulium sterilium lanceolata, subito longecuspidata per nervum excedentem et totum folii apicem replentem. Folia perichaetialia breviter acuta et vaginanter convoluta. Cellulae foliorum in

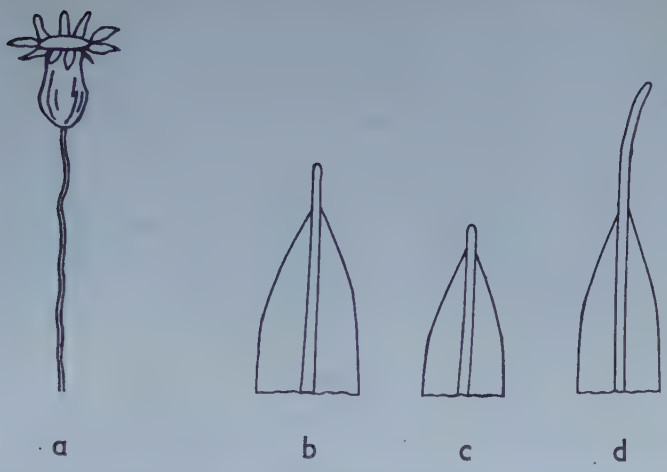

Fig. 1. *Seligeria groenlandica* n. sp. — a. kapsel med seta; b. och c. perichetialblad; d. stjälkblad.

parte latiore parenchymatosae, membranis crassis, superiores quadratae. In basi aliquae hyalinae, breviores latioresque, membranis tenuibus. *Capsula* (sicca) oblonga, sub orificio lato urceolata. *Peristomium* profunde insertum, longum, acutum. *Seta* angusta, torta, sed non curvata. *Sporae* exigue papillosae, 19—22 μ. — Holotypus in Herb. Mus. Paleobot. Stockholm.

Monoik. Tuvor brunsvarta till svarta, svagt kalkinkrusterade. *Stam* intill 25 m/m lång, förgrenad. *Blad* på sterila stjälkar lansettlika, hastigt långspetsade av den utgående nerven, som helt fyller bladspetsen. Perichetialblad kortspetsade och slidlikt omfattande. *Bladceller* i den bredare delen långsträckta, tjockväggiga; högre upp kvadratiska. I bladbasen några få hyalina, kortare och bredare samt tunnväggiga. *Kapsel* (torr) avlång, hopsnörd under den breda mynningen. *Peristom* djupt insererat, långt och spetsigt. *Seta* smal, vriden men ej krökt. *Sporer* svagt papillösa 19—22 μ (se fig. 1).

Seligeria groenlandica intar närmast en ställning mellan *S. lapponica* P. Nyman et W. Uggla och *S. polaris* Berggren men måste på grund av sina stora sporer föras till underavd. *Macrosporia* W. Uggla.

Från *S. lapponica* skiljes den lätt genom sina mindre sporer, sina mycket långspetsade blad, sin avlånga, ej tallriksformade kapsel (torr) och sitt långa peristom.

Från *Seligeria polaris* åter skiljer man *S. groenlandica* genom den senares större sporer, längre kapsel och långspetsade blad.

S. groenlandica växer uppenbarligen på ett substrat, som är kalkrikt, emedan tuvorna äro ganska ymnigt kalkinkrusterade. Det är att

hoppas, att framtida insamlingar skall vidga vårt vetande härutinnan, samt att man skall anträffa kapslar med *påsittande lock*, då lockets form särskilt med hänsyn till *sprötet* är av stor vikt. Även skulle då full klarhet nås beträffande *columellans* egenskaper.

Jag frambär mitt tack till dr Kjeld Holmen i Köpenhamn för hans vänlighet att sända mig ett prov av *Seligeria groenlandica*.

För översättning till latin av ifrågavarande beskrivning står jag i tacksamhetsskuld till överste Allan Uggla i Stockholm och för granskning av denna text till docent Åke Josephson i Uppsala.

Summary.

A New Species of Seligeria from Northern Greenland.

Dr J. Troelsen, Copenhagen of the Danish Peary Land Expedition 1947—50 to the northernmost Greenland has collected a new *Seligeria* species that is here described as *Seligeria groenlandica* W. Uggla. Its position in the system is between *Seligeria lapponica* P. Nyman et W. Uggla and *Seligeria polaris* Berggren.

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IDENTIFICATION OF POLLEN GRAINS AND SPORES IN LATE-GLACIAL DEPOSITS FROM GOTLAND, SWEDEN.

BY

J. TERASMÄE.

I. Introduction and some geological aspects.

The investigations of the history of vegetation have had great help of the advances in palynology. The advances in pollen and spore morphology have made it possible to identify a great number of fossil pollen grains and spores. And as a result of that our knowledge also of the history of the late Quaternary vegetation could be advanced considerably.

The present investigation will be a contribution to our knowledge of the history of the late-glacial vegetation of Gotland, Sweden. Furthermore, the results have been compared with other similar investigations from Scandinavia in the first place. The late-glacial vegetation is compared also with the present-day vegetation on Gotland, Öland, Götaland's calcareous localities and some localities in Estonia (cf. Fig. 1: B (black areas)]. A short survey is given in the following of some geological aspects of importance in this connection.

Gotland, the largest island of Sweden, occupies a central position in the Baltic. The small adjacent islands included, it comprises an area of about 3170 sq. km. (cf. also Pettersson, 1950). The nearest mainland coast lies at a distance of about 85 km.

The main features of the plane topography are controlled by the bedrock (cf. Munthe, 1913) consisting of Silurian strata. The limestones are of two principal kinds: hard cristallinic and soft marly ones (cf. Munthe, Hede and v. Post, 1925). Two dominating, broad ridges (NE-SW) follow the extension of the crystalline lime-

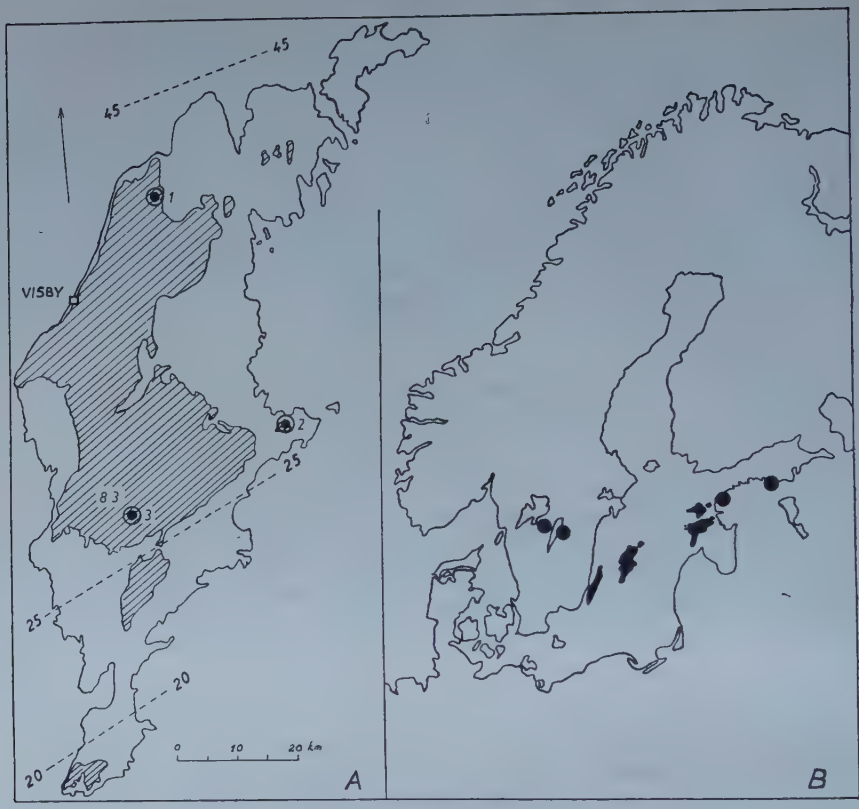
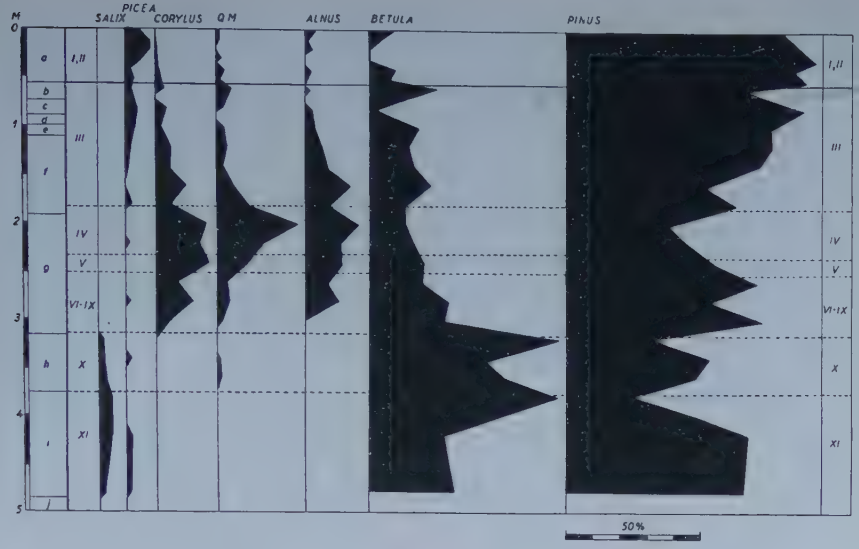
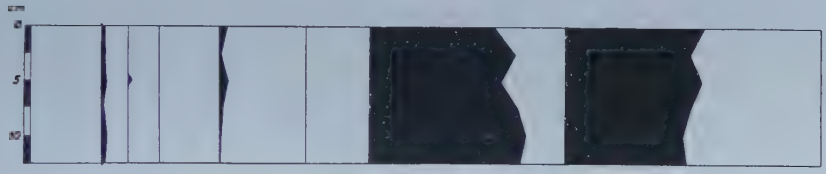


Fig. 1. A: a map over Gotland. The striated area is that not invaded by the Ancylus-trangression. The streched-lines mark the height (in meters) of the highest shore ridges of the Ancylus Lake above the present sea level; 1 — Vätlinge-mire, 2— Torsburgen-mire, 3— The mire near Lojsta, 83 — the highest point of Gotland. B: The areas taken into consideration marked with black.

stone, each reaching an altitude of about 83 m above sea leavel. The Quaternary deposits are often lacking and nearly everywhere relatively thin. No deposits of interglacial strata have yet been discovered. The glacial deposits consist of fluvioglacial material, clays and moraines, especially calcareous till containing numerous glacial erratics. The inorganic postglacial deposits are mainly coastal formations. The coarse material is often arranged in distinct shore ridges, some of which indicate postglacial transgressions of the Baltic, e.g. the Ancylus and Litorina transgression.

After the first stages of ice regression the Baltic constituted an ice-dammed lake, the Baltic Ice Lake, Gotland lying under the level of it. Afterwards, owing to land-upheaval and especially the drainage





YEARS B.C.	Geochronological periods by De Geer	Development of the Baltic by Munthe	Periods by Mohrén	Climatic periods in Sweden by Sernander	Pollenanalytical zones for Gotland by v. Post and Nilsson
5000	POSTGLACIAL PERIOD	LITORINA SEA	LITORINA PERIOD	ATLANTIC PERIOD	V
6000		ANCYLUS LAKE	ANCYLUS PERIOD	BOREAL PERIOD	VI VII VIII
7000	BIPARTITION				
	FINIGLACIAL PERIOD	YOLDIA SEA	YOLDIA PERIOD	SUBARCTIC PERIOD	IX
8000	DRAINAGE OF THE B.I.L. AT BILLINGEN		YOUNGER DRYAS PERIOD		X
9000	GOTIGLACIAL PERIOD	BALTIC ICE LAKE	ALLERØD PERIOD	ARCTIC PERIOD	XI
10000					
11000			OLDER DRYAS PERIOD		XII

Fig. 2. The uppermost diagram is one of the characteristic ones from Gotland, Martebomire [analysed by L. and S. von Post (1925); the drawing present made by I. Terasmäe]. The diagram below represents the pollenanalytical border between the zones IX and X from Torsburgen-mire. The table gives the schematic stages of the development of the Baltic-district (after Magnusson & Granlund & Lundqvist, 1949; Sveriges geologi).

of the Baltic Ice Lake at Mt. Billingen (central Sweden), Gotlands highest parts rose above the sea level. It is supposed that at that time Gotland was relatively higher above the sea level than nowadays (cf. MUNTHE, 1910, 1941). Further on the connexion between the Baltic and the Ocean over central Sweden was broken (owing to land-upheaval) and the Baltic was isolated again, constituting the Ancylus Lake. The short period between the Baltic Ice Lake stage and the Ancylus Lake is called the Yoldia Sea [salt water with the characteristic mussel Portlandia (Yoldia) arctica]. The highest parts of Gotland were left uninvaded by the Ancylus-transgression (cf. Fig. 1: A). It is supposed that a considerable part of the flora as well as the fauna invaded Gotland during the period of extremely low sea-level, before the Ancylus-transgression (cf. GISLÉN and BRINCK, 1950).

The conditions concerning Öland are quite similar to those of Gotland considered above.

The localities considered on the Swedish mainland are in most cases higher than the highest shore ridges (hence above the level of the Baltic Ice Lake).

The Estonian localities are of the same origin as those considered above. In the north the marked cliffs (klint) in calcareous rocks could be pointed out. Near the cliffs the Quaternary deposits are often lacking, the landscape constituting an »alvar». The bigger islands of Estonia (Saaremaa and Hiiumaa) are of the same nature as Gotland.

The mires investigated on Gotland are all higher than the shore ridges of the Ancylus Lake (cf. Fig. 1: A). The Vätlinge-mire is about 50 m, the Torsburgen-mire about 68 m and the mire near Lojsta about 40 m above the present sea level. The Vätlinge-mire is situated in a moraine landscape, the Torsburgen-mire on a plateau of limestone; the mire near Lojsta is situated beneath a marked cliff.

Finally I should like to take the opportunity to record my appreciation of the helpful cooperation, valuable advice and suggestions of Prof. G. E. DU RIETZ, Dr. G. ERDTMAN and Fil. lic. B. PETTERSSON.

II. Technique.

The deposits investigated consist mostly of calcareous mud and clay-mud. The amount of mineral particles increases downwards. Therefore treatment with hydrofluoric acid has been necessary. In that case the sample was at first treated with 5 % HNO_3, to get

rid of the chalk; after centrifuging and washing with water and alcohol, the sample was transferred to a copper crucible. Hydrofluoric acid was then added and the crucible placed in a fume chamber. At the palynological laboratory the sample is not heated when treated with hydrofluoric acid. A better effect seems to be had if the sample can be kept in a fume chamber for some days (now and then it must be stirred up). After centrifuging, decanting and washing with dilute hydrochloric acid and with glacial acetic acid, acetolysis was effected in the usual way (cf. Erdtman, 1943). In some cases the material was also chlorinated (with $NaClO_3 + HCl$; a few drops only of the chemicals).

Of the prepared material microscopical slides were made and the rest was preserved in conc. glycerine in small glass-tubes, for further control and new slides. The polliniferous material was closed in glycerine-jelly under the cover glass and paraffin was melted in around the glycerine-jelly. For doing that the slide was heated slightly and melted paraffin was added by means of a glass-rod. In some cases the polliniferous material in conc. glycerine was closed in under a cover glass in the same way. Then the pollen grains and other microfossils can be turned under the microscope for measurements by knocking slightly on the cover glass. During the microscopical investigations high power was used for all identifications.

III. Pollen grains and spores identified.

To identify pollen grains and spores one must have studied pollen and spore morphology and recent pollen grains and spores e.g. to be able to follow the descriptions and definitions given by pollen and spore morphologists (cf. Iversen & Troels-Smith, 1950). Furthermore, it is not enough to follow only the descriptions of pollen grains and spores, but the identified fossils must be compared, if possible, with the recent material, even »but a thorough study of the spores of the living groups is an indispensable necessity — in fact the actual basis — for the study of fossil spores». cf. Rao, 1943.

During my investigations I have had the great advantage of being able to use the comprehensive collection of recent spores and pollen grains of the Palynological Laboratory, Bromma. As help for identifications I have used the papers by Erdtman, Faegri & Iversen (1950) and the scattered literature available.

The pollen grains and spores identified from the late-glacial deposits are as follows.

Betula — The pollen material of *Betula* are quite heterogeneous in the late-glacial deposits. In a special investigation on the pollen morphology of *Betula nana* I will try to distinguish the pollen grains of tree-birches from those of *Betula nana*. A considerable part of the *Betula* pollen grains belong to *Betula nana*. A tetrad of *Betula* cf. *pubescens* has been observed.

Hippophaë rhamnoides — Pollen grains of *H. rhamnoides* occur in most of the samples with low frequency.

Juniperus communis — A few grains of *J. communis* have been observed in the younger late-glacial samples.

Pinus silvestris — In some slides deformities in the pollen grains of *P. silvestris* have been observed.

Populus tremula — A few grains of *P. tremula* have been identified.

Quercus — There are some pollen grains of *Quercus* observed in the younger late-glacial samples. They are different from those of *Q. robur*, but they cannot be distinguished from those of *Q. petraea*. In a paper (1948) Erdtman has given some characteristics on *Quercus* pollen grains. The pollen grains of *Q. petraea* are somewhat bigger than those of *Q. robur* subsp. *pedunculata*. The exine of *Q. petraea* is somewhat thicker and has a more distinct »spotting» (depending on the sexineous elevations). The bacula can be distinguished.

Ulmus — A few grains of *Ulmus* have been observed in the younger samples.

Salix — The pollen grains of *Salix* are present with a low frequency in most of the samples investigated. I have studied the pollen grains of recent Swedish *Salix* species. A special investigation of the pollen morphology of *Salix* will be published by H. Straka, Bonn. The studies he made at the Palynological Laboratory, Bromma, have made it possible to get an idea of the pollen grains of various *Salix* species. Pollen grains of *S. lapponum* have been identified. The resting *Salix*-material may consist of the following species: *S.* cf. *arbuscula*, *S.* cf. *glauca*, *S.* cf. *nigricans*, *S.* cf. *polaris*, *S.* cf. *reticulata*.

Artemisia — In most of the samples a considerable part of NAP consists of the pollen grains of *Artemisia*. The main part of the *Artemisia* pollen belongs to *A. vulgaris*. A few grains of *A. campestris*, *A. rupestris*, *A. maritima* and *A. absinthium* have been identified even. The pollen grains of *A. campestris*, *A. rupestris* and *A. vulgaris* have been described by Erdtman (1949).

The pollen grains of *A. maritima* are 3-colporate, subprolate - prolate-spheroidal (about 27×25 µ). Ora more distinct than these of other *Artemisia* species. Echini longer and more densely spaced than in e.g. *A. vulgaris*. Spinules vestigial or wanting.

The pollen grains of *A. absinthium* are 3-colporate, subprolate (about 25×22 µ). Echini more distinct than these of other *Artemisia* species. Spinules absent or indistinct. The pattern more rough and distinct than that of other *Artemisia* species.

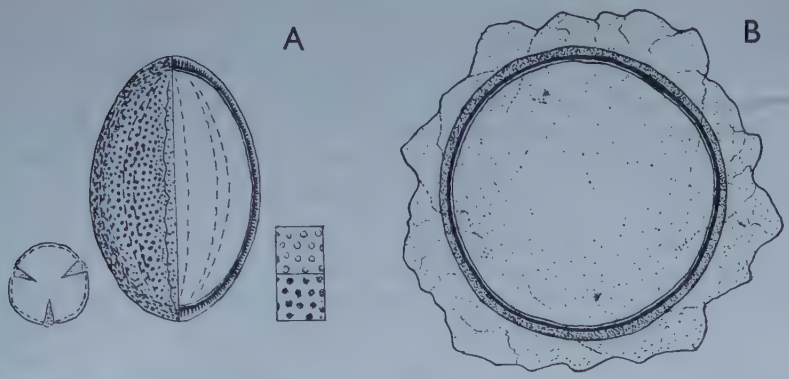


Fig. 3. A: Delphinium consolida (the drawing made after the scheme used by G. Erdtman). B: Equisetum limosum.

Chamaenerium angustifolium — Two pollen grains of that species have been identified.

Chenopodiaceae — Pollen grains of *Atriplex* and *Chenopodium* are present (cf. Faegri & Iversen 1950).

Compositae — A low frequency of pollen grains of *Liguliflorae* as well as *Tubuliflorae* is present.

Delphinium consolida (cf. Fig. 3: A) — The pollen grains of *D. consolida* are 3-colpate, prolate (-subprolate), about $35 \times 22\ \mu$. Sexine slightly thicker than nexine and somewhat swelled at poles. Pattern LO and distinct. The pollen grains of *D. consolida* are different from those of *D. elatum*.

Ericaceae — A few tetrads of *Calluna vulgaris* are present in many samples.

Empetraceae — Tetrads of *Empetrum nigrum* are present in most of the samples. Some of the tetrads, however, have been identified as these of *E. hermaphroditum*. The tetrads of *Empetrum* are, as noticed during the investigation, hardly distinguishable from those of *Ledum palustre*.

Gramineae — Pollen grains of *Graminae* are present with low frequency. Some grains of cf. *Elymus arenarius* have been identified.

Saxifraga aizoides — Pollen grains of *S. aizoides* are present with low frequency in samples from the Vätlinge-mire.

Cyperaceae — Pollen of *Cyperaceae* is present in all samples. Some distinctly elongated pollen grains of *Cyperaceae* may, perhaps, belong to *Scirpus* or *Schoenus*. Pollen grains of *Cladium* have not been noticed.

Stray pollen grains of following species have been noticed: *Asperula tinctoria* (?), *Filipendula* cf. *ulmaria*, *Nymphaea* cf. *alba*, *Potentilla* cf. *erecta*, *Sanguisorba minor*, *Saxifraga* cf. *oppositifolia*, cf. *Sedum acre*, *Thalictrum* sp., *Typha latifolia*, *Umbelliferae* (cf. *Heracleum sibiricum*).

Pteridophyta — Spores of following *Pteridophyta* have been observed: *Botrychium* cf. *lunaria*, *Cystopteris* cf. *fragilis*, *Dryopteris linneana*, cf. *D. filix-mas*, *D. thelypteris*, cf. *Ophioglossum vulgatum*, *Pteridium aquilinum*, *Lycopodium* cf. *complanatum* (cf. *alpinum*), *L. annotinum*, *Equisetum* cf.

limosum [the spores of *E. limosum* (cf. Fig. 3: B) are nonaperturate, spheroidal (diameter about 37 μ). Sexine as thick as or slightly thicker than nexine. The spores are provided with a thin indistinctly granulous perin. Often the spores noticed were separated from their perin.]

Furthermore fossils of *Hystrichosphaerideae* have been identified in older samples. As supposed by M. Fries [discussion of a paper by H. Brotzen (Geol. Fören. Förhandl., 73; 1: 149)] the *Hystrix* is an indicator of salt water conditions.

Spores of *Musci* (other than *Sphagnum*) and cf. *Hepaticae* (cf. e.g. Knox 1938, 1939) have been observed in many samples.

After qualitative investigations even percentages of different AP were calculated to place the investigated pollen spectra in the zoning for Gotland worked out by L. v. Post. In most of the samples only *Betula* and *Pinus silvestris* of AP are present. The *Betula* pollen frequency is about 20—35 per cent. This frequency is characteristic for zone XI (cf. Fig. 2). A diagram of some spectra from the Torsburgen-mire see Fig. 2. The connection between the pollenanalytical zones and the development stages of the Baltic are illustrated in Fig. 2. As to the pollen grains of *Artemisia* and *Salix*, there are about 2—3 pollen grains of *Salix* on about each 10 of *Artemisia*. Pollen grains of secundary origin are few in the late-glacial deposits from Gotland (the amount of secundary pollen grains in the late-glacial deposits seems to diminish towards the centrum of the glaciated area).

IV. Discussion.

In Sweden late-glacial pollen flora similar to that identified from Gotland have been described e.g. by Erdtman from Öland and Mt. Omberg (Östergötland).

From Öland the following pollen flora of Late-Glacial strata has been identified (Erdtman, 1946): *Betula, Corylus avellana, Hippophaë rhamnoides, Juniperus communis, Picea excelsa, Pinus silvestris, Salix; Artemisia, Chenopodiaceae, Cyperaceae, Galium, Graminae* (spont.), *Helianthemum, Peplis portula* and *Thalictrum*. Perhaps of secundary origin cf. *Ostrya* have been observed. *Lycopodium annotinum* (perhaps secundary) has been identified. Furthermore cf. *Anthemis*, cf. *Asplenium viride*, cf. *Chelidonium majus*, cf. *Dryas, Empetrum nigrum*, cf. *Filipendula*, cf. *Myricaria* and cf. *Saxifraga aizoides* have been identified.

From Mt. Omberg the following identifications (Erdtman 1949) may be mentioned: *Betula, Hippophaë rhamnoides, Juniperus communis, Picea excelsa, Pinus silvestris, Salix; Artemisia* (*A. vulgaris, A. rupestris*), *Astragalus alpinus, Chenopodiaceae, Compositae* (excl. *Artemisia*), *Cyperaceae, Ericales, Filicineae, Filipendula ulmaria, Gra-*

minae, Helianthemum oelandicum, Lycopodium, Orchidaceae, Petasites frigidus, Saxifraga cf. *oppositifolia, Selaginella, Umbelliferae.*

As to the late-glacial pollen flora from Denmark, England, Germany, Netherlands etc., the papers by FIRBAS, GODWIN, van der HAMMEN, IVERSEN and others have been considered.

It can be pointed out that from the Older Dryas period in the Netherlands, van der HAMMEN (1949) has identified a pollen flora with high *Artemisia* frequency and with pollen grains of *Helianthemum* (cf. *H. oelandicum*). In the same deposits a few pollen grains of *Sanguisorba minor* SCOP. have been identified by IVERSEN. Furthermore some fossils of »*Hystrix*» have been observed. *Sanguisorba minor* as well as *Hystrichosphaerideae* have been observed even in the late-glacial deposits from Gotland.

These pollenanalytical investigations in Sweden are corresponding with the macroscopical findings of plant remains in late-glacial deposits (cf. papers by e.g. ANDERSSON, HALLE, NATHORST, SERNANDER and others). Among these macrofossils identified from Gotland in deposits older than the Ancylus period the following may be mentioned: *Betula nana,* (*Betula* species other than *nana*), *Hippophaë rhamnoides, Juniperus communis, Pinus silvestris, Populus tremula, Salix herbacea, S. myrtilloides, S. nigricans, S. phylicifolia, S. polaris; Alisma plantago-aquatica, Arctostaphylos uva ursi, Cladium mariscus, Comarum palustre, Dryas octopetala, Empetrum nigrum, Hippuris vulgaris, Iris pseudacorus, Menyanthes trifoliata, Vaccinium uliginosum, Nymphaea alba, Phragmites communis, Pteridium aquilinum, Rubus saxatilis, Scirpus lacustris* (cf. MUNTHE, HEDE & v. POST, 1925).

With regard to the late-glacial pollen flora described above and to the recent pollen spectra from different plant communities (from Sweden cf. ERDTMAN, 1934 a, 1946, 1949), some similarities seem to be obvious concerning special localities. These special recent localities are of the following kind. In the first place the localities where the Quaternary deposits are thin or lacking. Furthermore the calcareous cliffs, some fluvioglacial ridges, Quaternary shellbearing deposits emerged by land-upheaval, emerged small islands and shores. The most important of these localities seem to be the bare calcareous ground termed »alvar» in Swedish. ALBERTSON (1950) has given the following characterization of it:

»Alvar ist ein geographischer Begriff, der ein waldloses Kalkheidegebiet bezeichnet, wo der von ordovizischen (oder auf Gotland silurischen) Kalksteinschichten aufgebaute Felsgrund oft zutage

tritt oder von einem dünnen Lager Verwitterungskies bedeckt ist. Bedeutende Teile des Gross-Alvar werden auch von glazialen Ablagerungen (Moräne, Glazifluvialkies) eingenommen, die oft hauptsächlich aus Urgesteinmaterial gebildet und dann ziemlich kalkarm (aber trotzdem eine nahrungsreiche Braunerde) sind; vgl. STERNER (1948, 1950).»

The calcareous ground on Gotland is classified by HESSELMAN (1908) as follows:

Bare ground — Quaternary deposits lacking. The karst-phenomena characteristic (cf. DU RIETZ 1921).

Calcareous ground with drained weathered deposits — This type is important on Gotland and has the Pinus silvestris forest as climax (cf. ALBERTSON 1946, p. 3).

Calcareous ground with undrained weathered deposits — The most important type on Gotland and Öland (cf. ALBERTSON 1946) characterised by violent frost action phenomena (cf. e.g. ALBERTSON 1946, STERNER 1926, TROLL 1944 p. 593—596).

All these types are present also in Estonian localities considered.

From the great southern alvar on Öland, ERDTMAN (1946) has identified the following recent pollen spectrum. One third of the total amount of pollen grains belongs to *Pinus silvestris*, another third consists of other AP than *Pinus* and pollen grains of *Juniperus communis;* the last third consists of pollen of herbs (pollen of *Graminae* in the first place followed by *Cyperaceae* and *Artemisia* and *Helianthemum*). More occasionally pollen grains of cf. *Anthyllis, Campanula, Compositae, Cruciferae, Galium, Geranium,* cf. *Herniaria, Leontodon autumnalis, Linum catharticum, Oxytropis campestris, Plantago, Ranunculaceae, Rosaceae, Scleranthus perennis, Secale* and cf. *Thymus.*

All the localities, the present flora of which is similar to the late-glacial flora from the same localities, are characterized by open conditions. These open conditions are due to special soil conditions. The wheathered layer of soil is very thin or lacking, and frost action phenomena are of considerable importance. The young tree-plants as well as the perennials cannot grow on that kind of soil. These open conditions of the landscape must have »survived» even the postglacial warmth-period (cf. ALBERTSON 1946, p. 15). No kind of closed forest or scrub vegetation has existed on the localities mentioned above. These localities constituted in the warm period re-

fuges for an alvar-vegetation, not capable of competing, that had immigrated at an early stage.'

The late-glacial pollen flora does not correspond to the present-day pollen spectra from forest-covered areas. It corresponds somewhat to the tundra and alpine-heath vegetation from northern regions (cf. e.g. Aario 1944, Erdtman 1949, Firbas 1949, Iversen 1947, Mitchell 1951).

Firbas (1949 p. 296—300) has characterized the following types of the late-glacial vegetation: »1. Grasheiden und Matten, 2. Gletscherweiden, 3. Strauchweiden, 4. Zwergbirken, 5. Sanddornbestände, 6. *Artemisia*-reiche Gesellschaften, 7. Zwergstrauchheiden, 8. Moos- und Flechtentundren.»

On p. 57 Firbas (1949) describes a »Tundrenartigen Glazialvegetation» and on p. 40 he writes: »Die engen ursächlichen Wechselbeziehungen zwischen Klima, Boden und Vegetation machen es veständlich, dass in der Natur bestimmten Vegetationstypen bestimmte Bodentypen zugeordnet sind.»

The problem of the character of late-glacial vegetation is an extremely complicated one. »It is noteworthy, though perhaps to be expected, that the tundra vegetation of central Europe during the late-glacial phases was of a considerably more complex type than that found to-day in tundra regions», cf. Deevey 1949 p. 1326. It has been compared with different recent plant communities and belts as considered above.

It is quite evident that the late-glacial vegetation was not homogeneous but consisted of different types and regions. It is impossible to compare it as a whole with some kind of tundra, alpine-heath, stepp or anything else. A certain succession of vegetation types may have existed even then. In spite of this it seems possible that, owing to a quite temperated climate, the alpine element and the stepp element of the late-glacial vegetation were somewhat mixed near the ice border. The climatic mean conditions may have been quite favourable, but the extreme cathastrophic changes of climate must have had a considerably higher frequency than they have now. Perhaps these conditions held the closed forest-vegetation at a distance, and a peculiar mixed vegetation existed near the ice border.

Could it not be of advantage to call the hitherto very little known phytogeographical belt near the ice border a »periglacial vegetation belt», where periglacial means the belt near the ice border and not only the ± narrow belt outside the area of the total glacia-

tion (cf. also Ray 1949)? More detailed investigations have proved that also the terms as late-glacial and postglacial should be used in a local and relative sense (cf. Deevey 1949 p. 1325—1326).

As pointed out by Faegri and Iversen (1950) »there has been a tendency among pollen analysts in different countries to consider curves of pollen diagrams as phenomena per se, as a kind of index fossils, and to utilise them independantly of their botanical background». Many experiments have been made to elucidate the late-glacial vegetation regions by means of the pollen diagrams constructed. As a matter of fact not many years ago only pollen of forest trees were investigated and first afterwards some herbaceous plants have been taken into consideration. Furthermore different pollen grains were confused with each other to a great extent (e.g. confusion between *Myrica-Corylus, Viola-Quercus, Salix-Fraxinus, Salix-Artemisia, Fagus-Helianthemum-Hippophaë, Corylus-Myrica-Urtica-Betula, Hedera-Lysimachia vulgaris* etc.; cf papers by Erdtman, Faegri & Iversen 1950 and others). Now we can distinguish all these types without difficulty. The different vegetation belts and climates cannot be distinguished by means of pollen diagrams but by means of the plant communities which supply the pollen spectra (cf. also Faegri 1945, p. 74 and Faegri & Iversen 1950 p. 82). It is the changes of plant communities we must know to draw conclusions on climate and ecology of plants etc. Therefore so many microfossils and macrofossils as possible must be identified to construct the ancient plant communities. The pollen diagrams generally used formerly should therefore be used in the first place for discussions on problems in Quaternary geology (for dating and connection purposes) for which they were worked out; cf. v. Post 1950, »but my main object was to get a method of geological time determination. This object has been achieved.»

I want to distinguish sharply between Quaternary-geological (geological) and botanical (vegetation-historical) pollen analysis (cf. also Erdtman 1944). The classical pollen analysis of von Post is an extremely well developed Quaternary-geological routine analysis and should be used as such. The botanical pollen analysis, on the other hand, is going through a rapid course of development. The working-out of methods etc. in botanical pollen analysis should be left to palynologists and phytobiologists, who will be able to develop it with greater success, as they have the necessary pollen-morphological, phyto-ecological etc. training.

One of the first important tasks in botanical pollen analysis is therefore to find the connection between recent plant communities and pollen spectra supplied by them. More exacting tasks cannot be undertaken until that is done.

March, 25th, 1951.

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THE ENDOSPERM IN SOME SPECIES OF CASSIA L.

BY

M. ANANTASWAMY RAU.

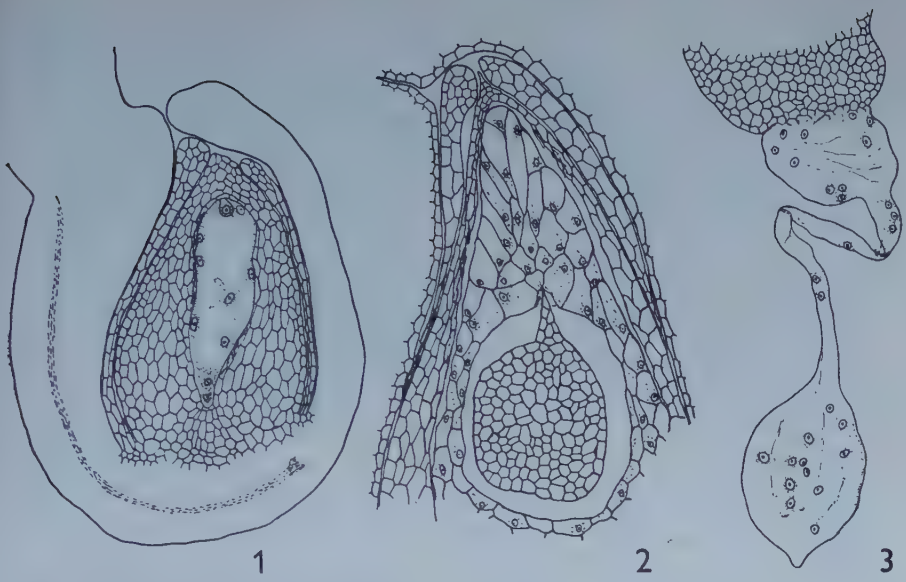
A study of literature reveals that very little information is available with regard to the post-fertilization development of the ovule in members belonging to the *Caesalpiniaceae*. As far back as 1860, Braun recorded the occurrence of an instance of polyembryony in a species of *Cassia* and Guignard (1881), in his comprehensive work, made a reference to the endosperm and embryo in a few species of the *Caesalpiniaceae*. Since then most of the papers that have appeared deal only with the development of the ovule up to the organization of the embryo sac. During an embryological study of several members of the *Leguminosae*, the author found an interesting type of endosperm formation resulting in the organization of a tubular process in *Cassia Tora* L., and this was reported in a note published recently (Anantaswamy Rau, 1950). In view of the interesting feature displayed by the endosperm, some more species of *Cassia* were studied. The results are described in the present paper. The following species have been investigated:

Cassia Tora L.,	*C. mimosoides* L.
C. occidentalis L.,	*C. siamea* Lam.
C. hirsuta L.,	*C. auriculata* L.

The material was collected around Mysore City, South India, fixed in formalin-acetic-alcohol and stained in Heidenhain's ironalum haematoxylin.

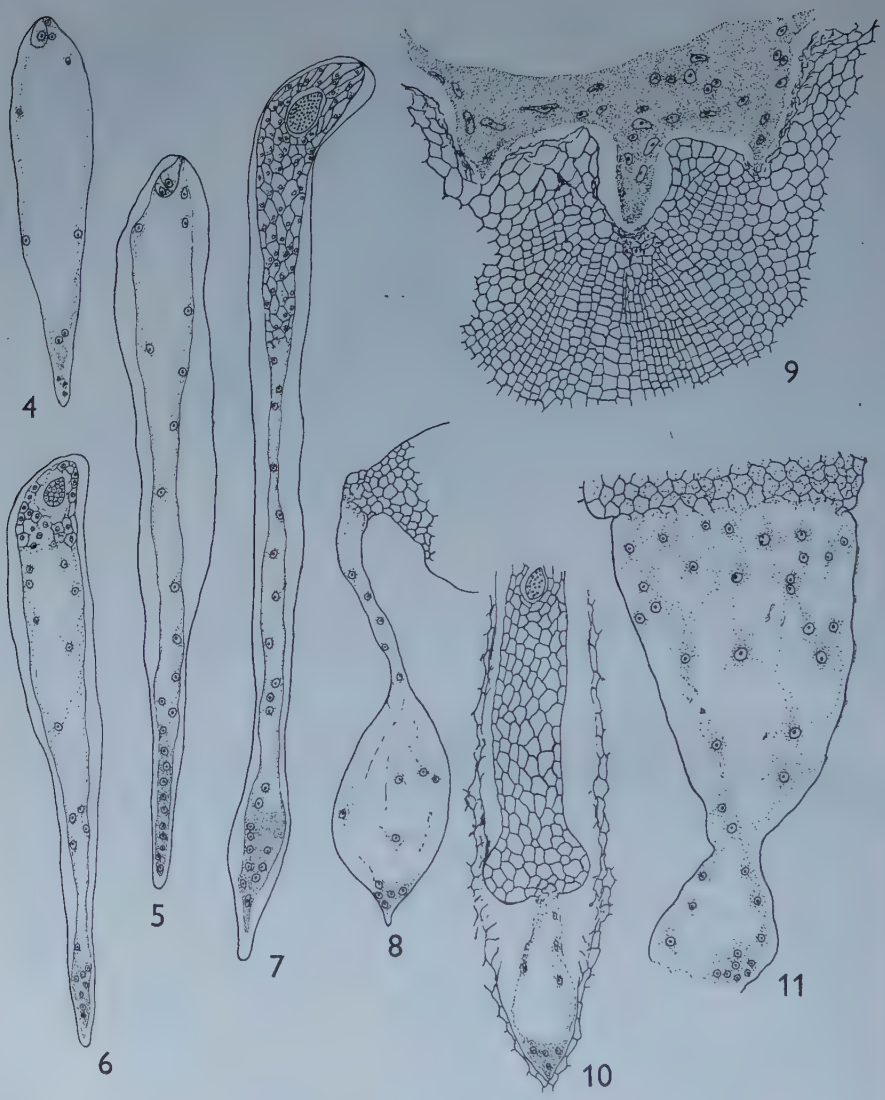
The Ovule.

The ovules are arranged on the marginal placenta and are anatropous but during later stages they show a tendency towards amphitropy. There are two integuments, the outer of which forms



Figs. 1 to 3. *C. mimosoides* L. Fig. 1. L. S. of ovule after fertilization showing different parts. × 100. — Fig. 2. Micropylar part of developing seed. Note elongated tubular cells of endosperm above embryo. × 100. — Fig. 3. Part of whole mount of endosperm showing chalazal tubular process. × 30.

the micropyle. At the time of fertilization, the ovule possesses the following structure. The outer integument is made up of three to four layers of cells and the micropyle is organized on the funicular side. The inner integument ends short of this and is made up of only two layers of cells along the sides but is thicker at the micropylar end. The nucellus is massive along the sides but gradually narrows towards the apex, ending in a cap-like structure which fits into the space in that region (fig. 1). The vascular strand of the funiculus that supplies the ovule ends in the chalazal region. In its neighbourhood, the cells are found to possess rich contents. After fertilization, the ovule enlarges considerably and some of the nucellar layers along the sides are disorganized on account of encroachment by the growing embryo sac. The inner integument gets completely crushed at the sides and can be seen only in the micropylar region. Its cells become modified here, acquiring thickenings on the walls. A darkly staining substance might also collect within them. The outer integument increases in thickness and starch grains in abundance are found in its cells. A meriste-



Figs. 4 to 8. *C. Tora* L. Stages in development of endosperm. Fig. 8 shows a part of whole mount of endosperm. Fig. 4 × 130; Fig. 5 × 100; Figs 6, 7, × 55; Fig. 8 × 30. — Fig. 9. *C. siamea* LAM. Chalazal part of seed showing meristematic zone, endosperm penetrating the chalaza. × 100. — Fig. 10. *C. hirsuta* L. L. S. showing cellular and free nuclear zones of endosperm. × 30. — Fig. 11. *C. auriculata* L. Part of whole mount of endosperm showing free nuclear portion. × 30.

matic zone is also sometimes seen in the outer integument at the micropylar end. Another feature of interest is the extension of the vascular strand to the outer integument during the post-fertilization stages. As has already been stated, at the time of fertilization, the vascular supply to the ovule stops short at the chalaza but with further development, strands of elongated cells appear in the outer integument and these organize themselves into vascular elements.

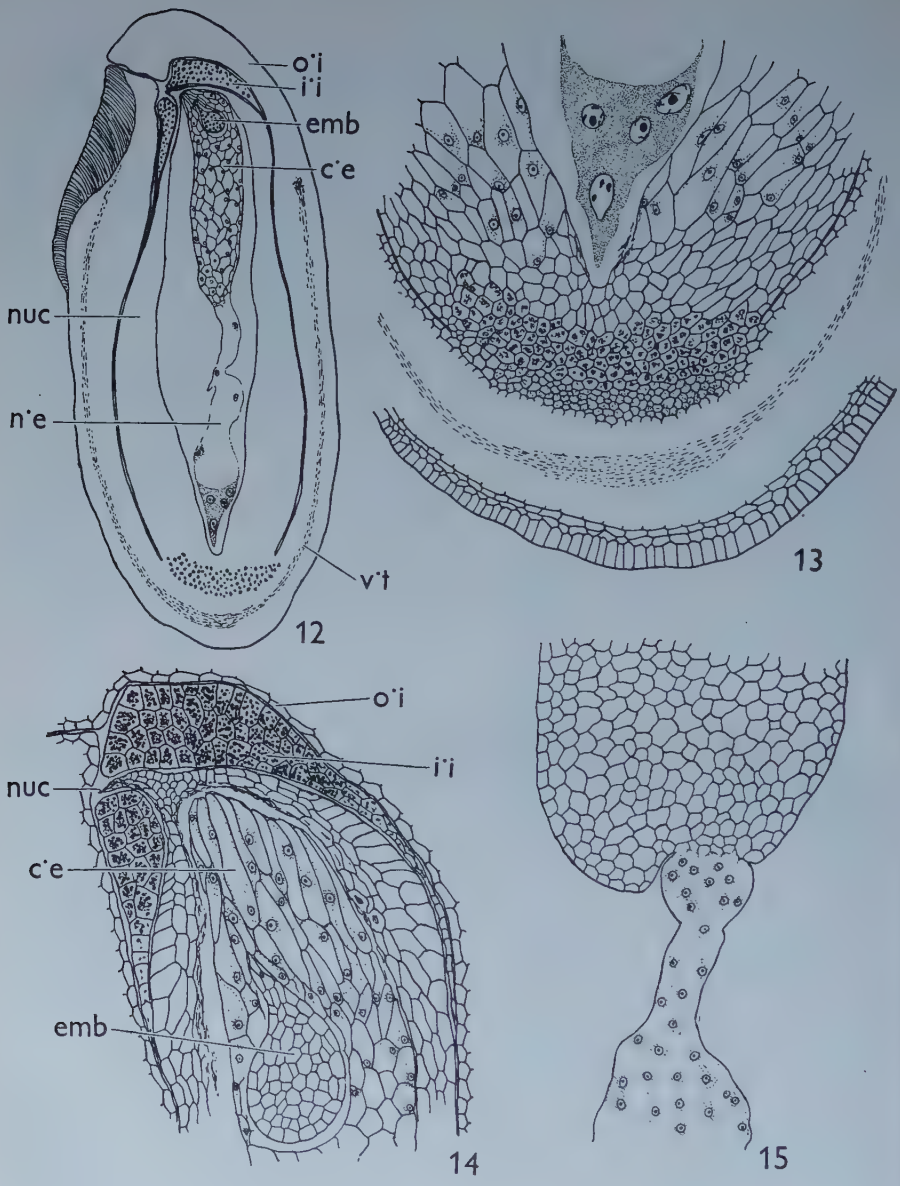
The chalazal region of the developing seed shows a rich nutritive zone and a hypostase is also organized. In *C. siamea*, considerable meristematic activity resulting in the formation of a prominent tissue is seen (fig. 9). Such a well developed meristematic zone at the chalaza has not been observed in any of the other investigated species.

The nucellus along the sides of the embryo sac is gradually disorganized and the nucellar apex shows a beak-like extension into the narrow passage formed by the inner integument (figs. 2, 14). In later stages the nucellus is completely crushed at the micropylar region.

The Endosperm.

The primary endosperm nucleus by repeated division gives rise to a number of free nuclei which are more or less uniformly distributed throughout the embryo sac. Subsequently one of the nuclei situated at the chalazal end becomes surrounded by denser cytoplasm and this region hereafter becomes more prominent. The embryo sac will be elongating in the meantime and the number of free nuclei at the chalazal end increases. Also the cytoplasm becomes very dense. This is very clearly to be seen in all the species examined. The elongation of the embryosac is most marked in *C. Tora* and *C. mimosoides.*

The fertilized egg divides only after a large number of endosperm nuclei have been formed. When the embryo has reached a many-celled condition, cell formation commences in the endosperm in the neighbourhood of the embryo (fig. 6). Wall formation takes place only in the micropylar part and the chalazal part remains free-nuclear. In *C. Tora* and *C. mimosoides* (figs. 3, 8), the chalazal part of the endosperm forms a narrow tube which shows a sac-like portion at its end. The stages leading to the formation of the



Figs. 12 to 15. *C. occidentalis* L. Fig. 12. L. S. of developing seed showing different parts. Note vascular tissue of outer integument. × 30. — Fig. 13. Chalazal part enlarged from fig. 12. × 100. — Fig. 14. Micropylar part enlarged from fig. 12. × 100. — Fig. 15. Part of whole mount of endosperm. × 30. — (*o.i.*, outer integument; *i.i.*, inner integument; *nuc.* nucellus; *emb.*, embryo; *c.e.*, cellular zone of endosperm, *n.e.*, nuclear zone of endosperm; *v.t.* vascular tissue).

tubular process in *C. Tora* are represented in figures 4 to 8. In this species, with the continued development of the seed and increase in the mass of endosperm tissue, the lower tubular process becomes irregularly coiled and twisted. Its sac-like end often gets displaced and may be found lying on one side or superposed over the cellular zone (Anantaswamy Rau, 1950). In *C. mimosoides* the tubular portion is even more prominent. One variation here is that next to the cellular zone a bulbous free nuclear portion is to be seen, the latter leading on to the tubular process which again shows the sac-like structure at its end (fig. 3). In the above two species the entire endosperm can be easily removed from the seed and the whole mounts show clearly the interesting tubular process. Serial microtome sections fail to give an adequate idea of this.

In *C. occidentalis* (figs. 12 to 15), next to the cellular zone, there is a slightly enlarged free nuclear portion but the tubular portion is very short. The chalazal end of the endosperm shows considerable activity and very dense cytoplasm with enlarged nuclei can be seen (fig. 13).

In *C. siamea*, the cellular part of the endosperm leads on to a cylindrical free nuclear portion which further broadens at the chalazal end. Here a very interesting activity of the endosperm is to be seen which has not been observed in the other species. As already stated, the chalazal tissue is very prominent with considerable meristematic activity and as a consequence a rich nutritive zone is organized. A large number of free endosperm nuclei are seen to gather in this region and the cytoplasm is also very dense. The antipodal end of the embryosac is wedged in the chalazal tissue and the endosperm penetrates into the chalaza at other points as well. The cells in this region are crushed on account of this encroachment (fig. 9). The endosperm thus assumes an absorptive haustorial rôle at the chalazal end in *C. siamea*.

In the other species examined, *C. hirsuta* and *C. auriculata* (figs. 10, 11), no distinct tubular process is organized. The endosperm clearly shows an upper cellular and a lower free nuclear region, however. The collection of free nuclei surrounded by dense cytoplasm at the chalazal end is to be seen here too.

At the micropylar end, the cells of the endosperm above the embryonal region become elongated and tubular (figs. 2, 14); they help to supply nutrition to the developing embryo. The endosperm tissue increases in the later stages and is then occupying

most of the embryo sac cavity; the free nuclear zone towards the chalaza disorganizes. The embryo has consumed only part of the endosperm when the seed has reached maturity.

My thanks are due to Prof. P. MAHESHWARI of the Delhi University for kind encouragement and help in connection with this investigation.

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TWO NEW ERIOPHORUM HYBRIDS FROM NORTH-EASTERN NORTH AMERICA.

BY

MARCEL RAYMOND.

There appears to be more hybrids in the genus *Eriophorum* than had at first been suspected. As in *Carex*, its species hybridize rather freely. In 1933, Sørensen quite accurately described an *E. angustifolium* var. *triste*[1] × *E. Scheuchzeri* from Greenland (Sørensen, 1933) which has recently been named × *E. Sorenseni* (Raymond, 1950). Four years later, *E. polystachio-vaginatum* was described from France (Beauverd, 1937). In the early part of 1950, *E. angustifolium* × *E. Scheuchzeri* was reported from northern Ungava and Alaska as × *E. Rousseauianum* (Raymond, 1950). Its general aspect is that of *E. angustifolium*, with a single spike set apart from the main group and borne on a long peduncule. This hybrid occurs rather frequently where the two species meet. A propos, more than a century ago, E. Meyer examined such plants: »Plurima speciminum labradoricorum spicam offerunt unam accessoriam, ex folii superioris acilla profectam, et reliquis multo longius pedunculatam . . .» (Meyer 1830).

I propose to present two new cases here, the first one being:

× ***Eriophorum Pylaieanum*** Raymond, hybrida nova.

(*E. spissum* Fernald × *E. russeolum* Fries)

E. fulvum La Pylaie, in sched. Herb. Mus. Paris. — *E. vaginatum* var. *Lapylaisi* Beautemps-Beaupré in sched. Herb. Mus. Paris. — *E. vaginatum* γ *perigynii pilis fulvis* Hooker, Fl. Bor. Am. II: 231. 1840, in part. — *E. callitrix* var. *erubescens* Fern., Rhodora 7: 85. 1905. — *E. spissum* var. *erubescens* Fern., Rhodora 27: 209—210. 1925. Gray's Man. of Botany (8th ed.): 279. 1950; Rouleau, Enum. Pl. Vasc. T. N., Contrib. Inst. bot. Univ. Mont-

[1] Now *E. triste* (Fries) Hardač & Löve (Löve, 1950), with a wide arctic distribution and 2 n = 60, while *E. angustifolium* has 2 n = 58.

réal, 64: 68. 1949. — *E. russeolum* Fries in Hartm., Handb. ed. 3: 13. 1838, in part. — *E. Chamissonis* Fries, non C. A. Meyer, Mant. Altera: 1—2. 1839, in part. (erroneously as *E. fulvellum* in both places).

Planta caespitosa; culmis numerosis 24—50 cm. altis saepe cum duabus vaginis, imam setoso-laminatam, ultimam vix inflatam, paulum fulvam cum margine nigro; foliis filiformibus subscabris culmis subaequalibus; spicula unica 15—20 mm longa, 15—20 mm lata, rotundata; squamis 7 mm longis, 2 mm latis, triangulato-anguste-lanceolatis, imis albis, ultimis cinereis, paulum reflexis; achaeniis 3 mm longis, 1.5 mm latis, obovatis, fuscis, mucronulatis; setis hypogyneis rufescentibus, 12—15 mm longis; antheris eburneis 1—1.2 mm longis.

St. Pierre and Miquelon Islands, Newfoundland, coastal sector of Saguenay County, Quebec, and adjacent Labrador.

Abbreviations for the different herbaria cited below are as follows:

MP. Muséum d'Histoire Naturelle (Paris, France);
KG. Herbarium of Kew Gardens (Surrey, England);
BM. British Museum of Natural History (London, England);
GH. Gray Herbarium of Harvard University (Cambridge, United States);
HH. Herbarium of the Botanical Institute of Helsinki (Finland);
NH. National Herbarium (Ottawa, Canada);
DA. Herbarium of the Dept. of Agriculture, Exp. Farm (Ottawa, Canada);
RM. Herbarium of the Naturhistoriska Riksmuseet (Stockholm, Sweden);
MV. Marie-Victorin Herbarium (Montréal, Canada);
JB. Jardin botanique de Montréal (Canada).

Saint-Pierre and Miquelon: *La Pylaie.* 1816 (TYPE in Muséum d'Histoire Naturelle de Paris). Also in KG, ex herb. J. Gay. — Anse à Pierre. 16.6.50. *Mathurin Le Hors* (JB); Ibid. 5.7.50 (JB). — *Delamarre*, 1882 (MP).

Newfoundland: *Beautemps-Beaupré* (MP); *Cormack.* 1822. (KG); *Despréaux.* 1828, in part. (MP, BM); *La Pylaie.* 1816. All without precise localities. — St. Barbe: Flowers Cove. *Priest E-4* (GH). — Old Port au Choix. *Fernald, Long & Fogg 1358* (GH). — Savage Cove (east of). *Fernald, Wiegand, Pease, Long, Gilbert & Hotchkiss 27 559* (GH). — Cow Head. *Fernald & Wiegand 2737* (GH). — Woody Point (back of). *Kimball 71* (GH). — Humber: Blomidon Range. *Stewart 26* (GH, NY). — Frenchman's Cove: bog about 2 miles inland. *Mackenzie & Griscom 10111* (GH). — Governor's Island. *Eames & Godfrey 5893* (GH). — Goose Pond. *Fernald & Wiegand 2735* (GH, NH). — Mt. Steepmore (or Seemore). *Fernald & Wiegand 2736* (NH). — St. Georges-Port au Port: Tompkins. *Pease & Edgerton 27233* (GH). — Grand Codroy River: tundra near Overfall Camp. *Pease & Edgerton 27161* (GH). — Grand Falls-White Bay. White Bay. St. Anthony: east slope of Fishing Head. *Abbe 117* (GH, RM); *Tuomikoski 172* (HH). — Quirpon Island. *Fernald & Long 27560* (GH, BM). — Grand Falls: Millerton Junction. *Fernald, Wiegand & Darlington 4724* (GH). — Quarry (near). *Fernald, Wiegand & Bartram 4723* (GH, RM, KG, NH). — South side of Gander, east side of

Island. *Bassett 395* (DA); *396* (DA). — St. Johns-West Placentia-St. Marys: Placentia. *Ayre* (GH). — Hogan's Pond, near Windsor Lake. *Tuomikoski* (HH). — Burin-Burgeo. Burgeo-Lapoile: Port aux Basques (back of). *Fernald, Long & Dunbar 26336* (GH); *Tuomikoski 78* (HH). — Channel. *Howe & Lang 899* (GH, NY). Type of *E. callitrix* var. *erubescens*. — Micmac settlement near St. Albans. Bay Despair. *Mathurin Le Hors*. 12.7.50 (JB). — Harbour-Main-Bell Island: Black Ridge, Holyrood. *Tuomikoski 26* (HH), *28* (HH).

Labrador: Blanc-Sablon. Noted by FERNALD as abundant[1]; no herbarium specimens.

Quebec: Saguenay Co.: Kegasca. *Lewis 01255* (NH). — Harrington Harbour. *Lewis 28477* (NH). — Rocky Bay. *Lewis 01256* (NH).

According to reports in literature (i.e., FERNALD 1911) and to Dr. ERNEST ROULEAU, who has so far spent two seasons in Newfoundland, this plant is always found where the two alleged parent-species occur. It produces perfect akenes and some, brought back from Newfoundland by Dr. ROULEAU, have been sown at the Montreal Botanical Garden early in 1951.

First noticed by BACHELOT DE LA PYLAIE (1786—1856) who marked it to for a new species, this striking plant has nevertheless had, like nearly all the species of *Eriophorum*, a very intricate story.

When FRIES published *E. russeolum* for the first time, in HARTMAN's Handbok i Skandinaviens Flora (1838), he cited *E. fulvum* La Pylaie (as *E. fulvellum*) as a synonym. The following year, in *Mantissa altera*, he abandoned his name when grouping all species with fulvous bristles under *E. Chamissonis* C. A. Meyer: the caespitose »species» of LA PYLAIE, as well as the two distinctly stoloniferous *E. russeolum* Fr. (*E. Chamissonis* of FERNALD and American botanists) and the true *E. Chamissonis* C. A. Meyer (*E. medium* Anderss. of Scandinavian botanists and *E. Chamissonis* var. *aquatile* of FERNALD).

FRIES explained (Mant. II: 2. 1839): »Quod *E. gracile* inter *E. polystachya*, hoc inter *vaginata* et si illa in unam speciem, suadente LAESTADIO, reduxeris quod vero a paucis approbatum fingimus, etiam *Eriophora vaginata* conjungere constans est. Lana russeola primo obtutu ab *E. vaginato* distinguit, sed *Eriophorum capitatum* variat lana rubella. — Quattuor diversis locis zonae arcticae eodem tempore detectum fuit; nempe in Newfoundland (*E. fulvellum* La

[1] »The bogs were everywhere brilliant with Cotton Grasses, *Eriophorum angustifolium, gracile, tenellum* and »*callitrix*», but handsomest of all the splendid bronzetopped »*E. Chamissonis*», and, its known range now extended across from Newfoundland, the recently described *E. callitrix*, var. *erubescens* Fernald». (Rhodora, 13: 123. 1911.)

Pylaie), in ins. Aleuticis, Siberia et Lapponia. Reliquis nominibus nondum divulgatis *E. russeolum* diximus, quod vero nomen lubenter alio publicato supprimimus, ne inutilis synonymia augeatur.»

But he revived his species in 1843, about which he wrote: (Mantissa III: 170. 1843): »Gracillima species gregis, haud caespitosa. Priscum meum nomen restituendum est, postquam ab *E. Chamissonis* C. A. Meyer, ab Auctore accepto, valde diversum reperi. Hoc, nempe C. A. Meyer, est omnino *E. capitatum* Suecorum, quo *E. capitatum* C. A. Mey. longe tenuius. Secundum speciminae loco indicato visa ad *E. russeolum* pertinet *E. vaginatum* γ Hook. Am. bor. p. 231., sed vegetatio diversa reliquique characteres ditissimo Viro effugerunt.» Hooker's *E. vaginatum* γ was La Pylaie's plant, something entirely different and, consequently, further disturbing the picture.

Nylander (1852) and Fernald (1905) cited *E. fulvellum* La Pylaie in synonymy: the first under that of *E. russeolum*, the latter, *E. Chamissonis*. Moreover, in his paper, Fernald described anew La Pylaie's very plant as *E. callitrix* var. *erubescens* (Fernald, 1905), which he later transferred to *E. spissum* (Fernald, 1925). He wrote then:

»The tendency of the pits of the rachis to ascend and the accompanying tendency to less depressed fruiting spikes along with the highly colored bristles suggest the possible specific distinctness of var. *erubescens*. The achenes, however, seem inseparable from those of typical *E. spissum* although they are sometimes inclined to be more slender. No flowering specimens of var. *erubescens* have been seen and the anthers are not known the plant being already in full maturity in July when botanists usually visit Newfoundland.»

Flowering specimens from Newfoundland have recently been provided by Dr. Risto Tuomikoski (University of Helsinki), who at present is engaged in work on the bryophytes of Newfoundland and the St-Pierre and Miquelon Islands, and by Dr. Mathurin Le Hors, a good student of the flora of the French Islands where he resides. The anthers are pale yellow, borne on capillary filaments. They mesure 1—1.2 mm.

One assumes that it is the *E. russeolum* »blood» which gives the spike its colour and its more elongate aspect, as well as the reddish tint of the stem below the sheath.

La Pylaie's notes on the type-specimen reads: »*E. fulvum* nobis. *Color ut in erioph. virginicae quae rufescens, nullusque huic in Europa similis.* Cette espèce assez commune dans les marais de l'île St Pierre

de Miquelon, avec les sarracénies etc., devient plus rare dans le nord de Terreneuve et se trouve à peine dans les marais que avoisinnent le havre de la station. De la Pylaie à Terreneuve 1816. Par 51 degrés de Lat. Bor.»

The library of the Montreal Botanical Garden has a microfilm copy, furnished by the Muséum d'Histoire Naturelle in Paris, of La Pylaie's voluminous (over 1000 pages) manuscript, entitled *Essai sur la flore de Terre Neuve et des îles St Pierre et Miclon exposant avec détail les caractères,* etc. In there, one finds, together with many beautiful plates he himself drew to illustrate his book, a more detailed description of his »species»:

Linaigrette fauve. Eriophorum fulvum n. [page 271].

E. culmo monocephalo breviore, foliis altiori, basi vaginato, folia filiformi-triquetra, rigida cartilagineo-denticulata. Spica minor, subglobosa, squamis latiuscule acuminatis. Setae insigniter sericeo-fulvae.

? Varietas forsan Er. vaginat. antecedentis.

La couleur des soies de cette plante ne diffère nullement de celle de l'*Erioph. virginicum*, dont on pourrait la prendre pour une variété au premier abord, mais dans l'e[s]pèce américaine, les chaumes sont cylindriques, et l'épi, en tête globuleuse, qui la termine, ne forme une seule masse que par le rapprochement intime des épis partiels dont elle se compose. Celle-ci croît non seulement dans la Virginie, mais encore dans la Caroline et même dans le Canada: aux environs de Québec[1].

L'Europe ne produit aucune espèce dont les soies aient une couleur analogue[2]. Quoique la touffe soyeuse des épis, jointe à des proportions inférieures à celles de l'*Erioph. vaginatum* semblent établir comme espèce notre *Erioph. fulvum*, j'hésite véritablement à la considérer comme tel, marquant qu'il offre du reste avec celui-ci, une conformité générale dans ses caractères essentiels.

Les feuilles de cette plante égalent en largeur les longues feuilles de l'autre espèce qui atteignent jusqu'à 25 centim. tandis quelles n'en ont ici que de 11 à 16 de longueur le plus communément, mais elles en diffèrent en ce qu'elles sont plus manifestement triangulaires jusqu'à leur sommet, cartilagineuses, denticulées sur leurs bords dans toute leur longueur, au lieu de l'être seulement vers leur extrémité supérieure; en outre ses chaumes ne portant que 2 gaînes, sont moins grêles; plus fermes et un peu plus élevés proportionnellement, au dessus des feuilles. Quant à la structure des gaînes je n'ai remarqué dans celles-ci aucune différence notable. Le chaume long de 12 à 21 centim. a son épi moitié moins gros, dont les cils sont d'un

[1] *Eriophorum virginicum* reaches the Côte-Nord, southern Labrador, Abitibi, etc. Michaux collected it near Quebec City.

[2] He apparently overlooked *E. russeolum* and *E. Chamissonis* which both grow in Northern Europe as well as in Newfoundland.

Fig. 1. *Eriophorum Chamissonis* C. A. Meyer. Mer Bleue, in the Ottawa district.

fauve soyeux presque doré et ses écailles aigues moins étroitement acuminées dans la majorité.

Cette plante est assez commune dans les marais de l'île St. Pierre-Miclon, et fort rare dans la partie nord de Terre-Neuve.

* * *

In 1942 Dr. A. E. Porsild described from Mer Bleue, near Ottawa, *E. opacum* var. *cinnamomeum*. He has kindly allowed me to see the original collection and given me duplicates of it. It is a plant close to × *E. fulvum*, but much larger, with setae of a pale cinnamon colour.

Now, only one species with rufous bristles exist in this bog. It is *E. Chamissonis* C. A. Meyer (Fig. 1), known from there since the time of Macoun and Fletcher; also only one cespitose species: *E. spissum* (*Porsild 6413*. NH. JB).

Fig. 2. × *Eriophorum Porsildii* Raymond. Mer Bleue, in the Ottawa District.

E. Chamissonis C. A. Meyer has, as main caracteristic features, the big sterile basal scale, stoutness, and the pale color of its bristles. The combination groups in various ways the different characters of both species. However the resulting plants are sterile. I have not found any well-shaped akenes. I propose to call the plant:

× ***E. Porsildii*** Raymond, hybrida nova (Fig. 2).

(*E. Chamissonis* C. A. Meyer × *E. spissum* Fern.).

E. opacum var. *cinnamomeum* Porsild, Can. Field-Nat. 56: 112. 1942 (published in 1943).

Culmis 50—60 cm. longis modo subsolitariis, modo laxe aggregatis; vagina superioria inflata; foliis longioribus aut subaequantibus culmis; spicula unica, 15 mm. longa anthesi angusta oblonga, demum 30 cm. longa cum lanis copiosis 30 mm. longa, oblongo-obovata; antheris 2 mm longis; achaeniis ignotis; setis pallide-cinnamomeis; squamis 5 mm. longis, 3 mm. latis.

Ontario: Mer Bleue. Peat bog near Carlsbad Springs. *Porsild 6430* (TYPE in NH, Isotype in JB Herbarium). — Mer Bleue. Peat bog near Ottawa. *Porsild 6414* (NH, JB). — In the Mer Bleue. Eastman's Springs. *Macoun 689* (DA).

In North America, *E. russeolum* appears to be oceanic (Löve, 1948), while *E. Chamissonis* is continental. Owing to the confusion created in North America over the two species, maps of both should be drawn anew. The locality indicated in Löve's map for *E. russeolum* should be erased, as the plant involved belongs to *E. Chamissonis* C. A. Meyer (*E. medium* Anderss. et auct. scandin.)

The chromosome number of *E. russeolum* is 2 n = c. 58. Those of *E. Chamissonis* and *E. spissum* are unknown.

The author wishes to thank Dr. A. E. Porsild, of the National Herbarium (Ottawa); Mr. J. A. Calder of the Division of Botany and Plant Pathology of the Department of Agriculture (Ottawa); Dr. Risto Tuomikoski, of the Botanical Institute of the University of Helsinki; Dr. Paul Jovet, of the Muséum d'Histoire Naturelle (Paris); M. Mathurin Le Hors, from St Pierre and Miquelon; Dr. Jacques Rousseau and Mr. James Kucyniak of the Montreal Botanical Garden, as well as Dr. Ernest Rouleau, of the Institut botanique de l'Université de Montréal, for their appreciated help and advice.

Montreal Botanical Garden, Canada.

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SMÄRRE UPPSATSER OCH MEDDELANDEN.

Föreningens medlemmar uppmanas att till denna avdelning insända meddelanden om märkliga växtfynd o. d.

Dictyophora duplicata i Värmland.

Under en biltur genom Värmland i somras gjorde jag ett, som det senare visat sig, ganska märkligt svampfynd. På grundval av min strax efter fyndet gjorda avritning och beskrivning av svampen har professor J. A. Nannfeldt i Uppsala nämligen fastställt, att det utan tvivel rör sig om *Dictyophora duplicata*, en släkting till vår vanliga stinksvamp *Phallus impudicus*. För 25 år sedan var *Dictyophora* endast känd ifrån östra Nordamerika, men har sedan förts över till Europa med importerade barrträdsplantor, så att den nu är funnen i både Tyskland, Danmark och Sverige (N. F. Buchwald i Dansk Naturhistorisk Tidende, Årg. 5, Nr 4, sid. 60—64). I vårt land har *Dictyophora* förut endast anträffats i Skåne (1948) på två lokaler, där den växte på örtrik, bördig mark i bokskog (O. Andersson, Botaniska Notiser 1950, Häfte 1, Lund).

Vid Fölsvik, strax öster om sjön Mellan-Fryken i Värmland växte svampen i ett skuggigt strandbuskage, bestående huvudsakligen av al, björk och gran. Jag lyckades dock ej finna mer än ett exemplar.

Jan Höjer.

RECENSIONER.

Johansen, Donald Alexander, Plant Embryology. Embryogeny of the Spermatophyta. — A New Series of Science Books edited by Frans Verdoorn. Vol. XXIV. Waltham, Mass. (The Chronica Botanica Co.; Uppsala: Lundequistska Bokhandeln) 1950. 305 sid. $ 6.00.

Embryologerna ha under senare år kunnat glädja sig åt att handböcker utkommit, som äro av stort värde för den högre akademiska undervisningen och underlätta specialistens arbete. Å. Gustafssons Apomixis in higher plants I—III av år 1946 och 1947 följdes år 1950 av P. Maheshwaris Introduction to the Embryology of Angiosperms och D. A. Johansens Plant Embryology. Medan Maheshwari förträffligt visar oss vägen inom alla huvudområden i angiospermernas embryologi, behandla de båda andra speciella avsnitt.

Johansens omfångsrika arbete skildrar embryot hos fröväxterna, det behandlar spermatofyternas embryogeni. I anslutning till bokens förteckning med definitioner över embryologiska termer förtjänar inledningsvis påpekas innebörden av författarens termer embryogeny, embryology och embryonomy:

Embryogeny: the origin, development, structure and functions of the embryo.
Embryology: That division of Plant Morphology concerned with all phases of embryogeny.
Embryonomy: Exposition of the laws of embryonic development.

Inledningen lämnar i ord och bild en historik, där namnen på embryologer från skilda epoker möta fram till heroer inom embryoforskningen som Souèges i angiospermernas rike och Buchholz i gymnospermernas. Därefter följer en redogörelse för de nakenfröiga växternas embryogeni, Cycadaceae-Welwitschiaceae, med underkapitlen befruktning, proembryo, embryo, ev. polyembryoni samt litteraturhänvisningar för varje familj. Så kommer det stora avsnittet om anthophyternas embryogeni. Det inledes med terminologiska frågor, där författaren lämnar klara distinktioner, han skildrar tidigare försök till embryonomisk klassifikation och övergår till lagar och formler. Anthophyternas sex embryonomiska huvudtyper (Piperad Type, Onagrad Type, Asterad Type, Caryophyllad Type, Solanad Type, Chenopodiad Type) med ev. variationer lämnas redogörelse för i ett kapitel, i vilket också Souèges' system presenteras och granskas. I anslutning till Hutchinsons system följer därefter det långa kapitlet om anthophyternas speciella och jämförande embryogeni. Familj efter familj genomgås och

litteratur anges. De följande avsnitten behandla apomixis, adventivembryogeni och polyembryoni. Därefter lämnas förklaring till embryologiska termer och följer register.

Det är givet, att JOHANSENS sammanfattande, stora arbete över fröväxternas embryogeni är att hälsa med stor glädje. Författaren har själv för några årtionden sedan utgivit morfologiska arbeten om onagracéer och har oberoende av SOUÈGES uppställt system över anthophyternas embryotyper. Boken är mycket klart och redigt disponerad, tryckt på bra papper och försedd med många avbildningar. För varje embryolog innehåller den mycket värdefulla litteraturhänvisningar. Att i ett jättearbete som JOHANSENS få med en fullständig litteratur om embryot hos anthophyter är givetvis omöjligt, vilket också framgår av företalet. Den som intresserat sig för en eller annan växtfamiljs embryologi, finner lätt, att ett eller annat arbete, som är honom bekant och innehåller uppgifter om embryot, ej kommit med i bokens litteraturlistor. Vid studiet av de speciella avsnitten i JOHANSENS arbete finner man ganska snart, att få av våra forskare närmare intresserat sig för och lämnat noggranna bidrag av vägande art till kännedomen om spermatofyters embryoutveckling. Den kritik, som å s. 11 riktas mot tysk, svensk och indisk embryologi synes anmälaren onödigt hård och knappast motiverad.

Helge Stenar.

WIKÉN, ERIK, Latin för botanister och zoologer. — Gleerups, Lund 1951. 497 pp. Pris 24 kr.

Heter det *Cy'clamen* eller *Cycla'men?* Är *Erigeron* maskulinum eller neutrum, och bör vi alltså säga: *Erigeron canadensis*, eller: *E. canadense?* Inför dessa och liknande spörsmål ställes biologen säkert så gott som dagligen. I själva verket tillhör han den grupp av vetenskapsidkare, som näst klassikerna själva och jämte läkarna har den livligaste beröringen med det ärevördiga romarspråket. Han behöver det för sina diagnoser, och han brukar det i sin terminologi. Det är en stor brist, att en handbok, avsedd att tillgodose hans rättmätiga språkliga intresse, hittills icke förelegat på svenska. Genom lektor ERIK WIKÉNS nyligen utkomna Latin för botanister och zoologer har denna brist nu blivit avhjälpt.

Till det yttre framträder boken som en latinsk språklära. Förf. går kapitelvis igenom uttal och stavning, betoning, substantivens och adjektivens deklination, adverb, räkneord, pronomen, prepositioner, verbböjning och ordbildning. Verket avslutas med några latinska textstycken, bl. a. några prov på latinska diagnoser, försedda med rikhaltig kommentar, säkerligen ytterst värdefull för blivande auktorer.

Någon språklära av traditionell typ är det emellertid inte fråga om. På väsentliga punkter avviker den från skolgrammatiken. Av syntaxen har sålunda blott så mycket medtagits, som ansetts oundgängligt för den botaniska diagnosen. Det är framför allt kasusläran, som — inrymd i formläran — på detta sätt fått komma med. — Själva uppläggningen av de olika avsnitten är också en annan än den vanliga skolgrammatikens. Skolgossen skall lära sig den latinska formläran, biologen förutsättes komma att ta sin tillflykt till den huvudsakligen för att hämta sporadisk upplys-

ning. Hans grammatik bör därför främst ha karaktären av en överskådligt disponerad uppslagsbok. Ett exempel må belysa, hur förf. löst problemet. Skolgrammatiken indelar tredje deklinationens substantiv efter olika stammar. En sådan anordning skulle inte tillfredsställa biologen. Han skulle inte kunna hitta rätt i det oöverskådliga virrvarret (vilket av skäl, som nedan skall antydas, är flera gånger värre i det biologiska latinet än i det klassiska). Wikén går nu så till väga, att han företar en indelning i 19 klasser, icke efter stammar, utan efter ordslut i nom. sing. (*-or*, *-er*, *-ur* o. s. v.). Varje klass utrustas sedan med sina underavdelningar, och först här lägges stammen till grund för indelningen. Anordningen är praktisk. Den möjliggör för botanisten att examinera sina termer lika säkert, som han bestämmer en ört med hjälp av sin flora. Förf. har tagit lärdom av den vetenskap, vars språk han behandlar.

Wikén har vidare haft att ta ställning till den lagstiftning, varmed man i modern tid sökt reglera en vildvuxen nomenklatur. Botanister och zoologer har härvid understundom gått skilda vägar, en ytterligare komplikation för förf. Sålunda latiniseras personnamn på olika sätt i de båda fackspråken. De radikala zoologerna sätter *-us* till alla efternamn, utan hänsyn till dessas form. Botanisterna har efter bestämda regler än *-us*, än *-ius*. Utan tvekan är det de senare, som befinner sig i linje med god latinsk tradition. — Ett verkligt svårlöst spörsmål är frågan om släktnamnens genus. Förf. underkastar de gällande reglerna (de botaniska, zoologiska finns ju icke) en ingående analys och har åtskilliga anmärkningar att rikta mot dem. Så t. ex. saknas rekommendationer för de fall, där släktnamnet är en med latinskt eller grekiskt språkmaterial bildad modern avledning (ex. *Odont-ites*, subst., *Fum-aria*, substantiverat adj.). Förf:s framställning bildar på denna punkt en viktig komplettering till reglerna. Vidare tycks lagstiftarna inte ha haft klart för sig, att släktnamn i stor utsträckning måste betraktas som substantiverade adjektiv (jfr Dansers kritik i Blumea I, 1934—35). Deras rekommendation X (e) anbefaller rent av »to avoid adjectives used as nouns». Som en följd av denna inställning får man betrakta den egendomliga formulering, som den andra av deras genusregler har fått: »Generic names which are modern compounds formed from two or more Greek or Latin words take the gender of the last. If the ending is altered, however, the gender will follow it.» I kraft av denna regel skulle moderna släktnamn på *-chroma*, *-dema*, *-derma*, *-gala* o. s. v. bli neutra. Wikén visar nu upp, att sådana sammansättningar på grund av sin betydelse i kanske de flesta fall måste uppfattas som femininformer av substantiverade adjektiv. Det antika *Polygala* är femininum. En svårighet ligger däri, att samma slutled kan uppträda som komponent än i ett substantiv, än i ett substantiverat adjektiv. Algnamnet *Zygonema* är ett substantiv och följaktligen neutrum (algen är en tråd), angiospermen *Spironema* bär däremot ett namn, som är ett substantiverat adjektiv och därför har feminint genus (den är trådig). Ansikte mot ansikte med denna svårighet tvekar Wikén att föreslå en revision av regeln. En sådan förefaller mig likväl ofrånkomlig. Med tanken att lösa problemet genom att införa ett enhetsgenus för alla släktnamn (femininum för de botaniska, neutrum för de zoologiska) har jag dock svårt att förlika mig (*Chrysanthemum leucanthema?*).

Slutligen har Wikén haft att brottas med de problem, som uppstått genom det oerhört starka inslaget av grekiska ord och böjningsformer i det latin, han behandlar. Botanister och zoologer har ådagalagt en ännu större iver, då det gällt att tömma grekiskan på dess rika skatter, än medicinarna (vilka redan de är väl så goda greker som romare). Särskilt framträder detta i kapitlen om substantivens och adjektivens deklination samt givetvis i det om ordbildningsläran. De har alla fått ett betydande omfång. Att förf. lyckats bemästra det väldiga materialet, är en bedrift. Det tjänar väl inte mycket till att inför en naturvetenskapligt inriktad läsekrets gå in på enskildheter. Ett exempel må dock belysa, till vilka komplikationer detta ivriga språkliga botaniserande har fört. Ett ord som *actis* (sällsynt biform: *actin*), stråle, kan användas för att som slutled bilda följande olika typer av sammansättningar: 1) olikstaviga subst. efter 3 dekl.: *-actis*, gen. *-actinis;* 2) olikstaviga adj. efter 3 dekl. av två ändelser: mask.-fem. *-actis*, neutr. *-actin*, gen. *-actinis* (en för den latinska skolgrammatiken okänd typ, svår att böjningsmässigt komma till rätta med); 3) olikstaviga adj. efter 3 dekl. av en ändelse med konsonantstamböjning: mask.-fem.-neutr.*-actin*, gen. *-actinis* (en i det egentliga latinet sparsamt företrädd typ, även den formellt svårbemästrad); 4) adjektiv efter 1 och 2 dekl.: mask. *-actinus*, fem. *-actina*, neutr. *-actinum*. Man förstår förf., när han för bildning av adjektiviska sammansättningar förordar en inskränkning till den sistnämnda typen.

Av de smärre invändningar, som min lektyr föranlett, må följande förtecknas. Påståendet s. 32, att en vokals längd i hög grad beror på betoningen etc., rimmar dåligt med paenultimaregeln, som förf. ss. 43 ff. gör sig sådan möda att inprägla. Här har två principer kommit i konflikt med varandra: hänsynen till moderna språkvanor och hänsynen till det klassiska latinets normer. Jag ställer mig avgjort på de senares sida. — Indelningen av de hybrida orden s. 259 f. är icke lycklig. Läsaren får det intrycket, att förf. av rent formella skäl vill avråda från begagnande av vissa typer av sådana. Sålunda säges hybrida ord, i vilka ett grekiskt prefix står framför ett latinskt slutled (*parasacralis*) eller vice versa (*subdeltoideus*), vara direkt dåliga. Ur allmänt antik synpunkt är de säkerligen icke sämre än övriga typer. Jag antecknar ur min materialsamling: *epinomen*, *epiraedium*, *epitogium; subdiaconus*, *subsericus*, *subthronizo* och hela rader av sammansättningar med *con-*, *co-* etc. (företrädesvis senlatinska ord). Det finns alltså ingen anledning att sätta just dem i strykklass. Ur strängt klassisk synpunkt är de visserligen mindre önskvärda, men detta torde gälla samtliga hybrider (möjligen med undantag av typen *gastrula*). — Bruket av avledningsändelsen *-osus* i växtnamn som *Anemone nemorosa*, *Crepis paludosa*, *Myrtillus uliginosa* borde kanske ha stämplats som ett missbruk även s. 307 (där just detta suffix behandlas), icke blott ss. 282 och 360. — *Polygala* säges s. 372 »egentligen» betyda »mjölkrik», språkligt korrekt, men knappast sakligt. Som växtnamn betydde ordet redan i antiken »som framkallar mycket mjölk» (hos boskapen), Plin. Nat. Hist. 27, 121: *polygala, quae pota lactis abundantiam facit.* — Till sist vill jag framhålla, att boken är väl korrekturläst. Av mera besvärande tryckfel har jag blott upptäckt *fructiculus* för *fruticulus* s. 264 och svinhöna för svinböna s. 317.

Mitt slutomdöme om Wikéns verk blir: det är ett imponerande arbete, väl motsvarande både filologiska och, så vitt jag vågar döma, botaniskzoologiska krav. Varje enskild detalj i verket är utarbetad med en omsorgsfullhet, som man måste nämna beundransvärd. Såsom av det närmast ovanstående framgår, är det mycket svårt att hitta minsta lilla blotta i pansaret. Framställningen är genomgående klar och översiktlig. Allt detta gör, att boken kan på det livligaste anbefallas till flitigt studium. Den kommer att bli värdefull som rättesnöre och som incitament till fortsatt nyttig diskussion av viktiga terminologiska frågor.

Alvar Erikson.

Wulff, E. V., An Introduction to Historical Plant Geography. Auth. transl. from Russian by Elizabeth Brissenden. Rev. ed. — Waltham, Mass. (: The Chronica Botanica Co.; Uppsala: A. B. Lundequistska Bokhandeln) 1st print. 1943, 2nd print. 1950 (Orig. Russ. ed. Leningrad 1932). 223 pp., 35 figs. Pris $ 5.00.

Den floristisk- och historisk-växtgeografiska litteraturen har under senare tid berikats med inte mindre än tre stort upplagda handböcker, Wulffs »An Introduction to Historical Plant Geography», Cains »Foundations of Plant Geography» och Goods »Geography of the Flowering Plants». Dessa tre arbeten komplettera varandra på ett ganska lyckligt sätt: Wulff ger framför allt en teoretisk utredning av själva arealbildningen, dess olika typer och i någon mån av dess orsaker, Cain behandlar huvudsakligen de kausala grundvalarna för denna arealbildning med särskild hänsyn tagen till de grunddiscipliner på vilka den växtgeografiska forskningen måste bygga, medan Goods arbete främst är den stora exempelsamlingen för de fenomen som de två andra författarna sökt utreda.

E. V. Wulff, föreståndare för herbariet vid The Institute of Plant Industry, Leningrad, och numera avliden, utgav den första upplagan av detta arbete år 1932. En något reviderad edition utkom följande år. »An Introduction to Historical Plant Geography» var avsedd att bli den första delen av en trilogi, som skulle behandla den historiska växtgeografien ur vidast möjliga synvinkel. Del 2, omfattande de olika florornas historiska utveckling, förelåg i publiceringsfärdigt skick vid det andra världskrigets utbrott; om dess vidare öden är ingenting känt. En tredje del, behandlande växtgeografiska förändringar förorsakade av människan från äldsta till nuvarande tid, lär delvis ha förelegat i manuskript. Av det utkomna första bandet att döma torde förlusten av manuskripten till de två följande delarna få betraktas som närmast en katastrof.

Under krigsåren vaknade tanken på amerikanskt håll att göra Wulffs arbete tillgängligt även för de många växtgeografer som inte behärskar ryska. Den amerikanska editionen utkom 1943, sedan litteraturen och framställningen i samarbete med förf. bringats up to date. Drivande kraft bakom det hela var E. D. Merrill, som också försåg denna upplaga med ett kort företal. Arbetet, som hade tryckts i en begränsad upplaga, rönte stort intresse och efterfrågan och hade efter blott några månader slutsålts från förlaget. Av denna anledning och för att tillmötesgå talrika uttalade

önskemål ombesörjde »Chronica Botanica» en nytryckning år 1950, ett företag för vilket man har all anledning att vara förlaget tacksam.

Under alla de år som Wulff arbetade på detta sitt magnum opus, hade han föga kontakt med växtgeografer i andra länder. Krigsåren ökade ytterligare denna isolering som måste ha varit ett avsevärt minus vid utgivandet av ett sammanfattande arbete av denna art. Detta är särskilt märkbart när det gäller litteraturbehandlingen. Av den ryska litteraturen fram till 1943 har givetvis inga viktigare källor förbigåtts. Samma förhållande gäller i viss utsträckning centraleuropeiska forskningsresultat fram till det andra världskrigets utbrott. Två kategorier som däremot ytterst ofullständigt inarbetats i texten är dels europeiska arbeten utgivna under krigsåren — i viss utsträckning sammanfattade i det senast utkomna bandet av »Fortschritte der Botanik» — dels den betydande amerikanska litteraturen från 1930 och framåt. Sistnämnda lucka har i någon mån fyllts genom att U.S.A.-upplagan försetts med ett tillägg av H. M. Raup, där kompletterande uppgifter lämnats främst över sådana amerikanska arbeten som utkommit mellan 1932 och 1943.

Såsom ovan redan antytts är Wulffs framställning huvudsakligen ägnad arealer, deras uppkomst och utbildningstyper. De två första kapitlen ger en allmän översikt av den historiska växtgeografien, dess syfte, metoder och relation till vissa andra botaniska och geografiska vetenskapsgrenar (paleobotanik, taxonomi, paleogeografi, paleoklimatologi och historisk geologi) varjämte förf. lämnat en åtminstone för 1800-talet ganska fyllig framställning av växtgeografiens historiska utveckling. Wulffs egen definition av historisk växtgeografi framgår av följande uttalande: »Historical plant geography has as its aim the study of the distribution of species of plants now existing and, on the basis of their present and past areas, the elucidation of the origin and history of development of floras, which, in turn, gives us a key to an understanding of the earth's history.»

De tre följande avsnitten behandlar helt arealfrågor. I det första av dessa förekommer en utförlig redogörelse för de olika typerna av utbredningscentra (centers of frequency, c. of maximum variation (primary and secondary), c. of dispersal) och deras relativa betydelse vid tolkningen av arealernas uppkomst och de taxonomiska enheternas fylogeni. Szymkiewicz' undersökningar över variationscentra refereras särskilt utförligt. Samma kapitel behandlar också arealgränser. Förf:s indelning av dessa i topografiska, ekologiska och biotiska gränser innebär emellertid en utomordentligt stark schematisering. I detta sammanhang kommer Wulff också in på Willis' bekanta teori om »age and area», vilken refereras liksom de talrika motargumenten.

I sin följande ytterst kortfattade redogörelse för utbredningsområdenas uppkomst behandlar Wulff i detalj huvudsakligen endast den gamla tvistefrågan om arealernas monotopa eller polytopa ursprung. Möjligheten av det senare alternativet avvisas med bestämdhet. — Det tredje av dessa kapitel beskriver några principiella utbredningstyper (endema, vikarierande, relikta, kontinuerliga och diskontinuerliga typer) och lämnar slutligen en utförligt kommenterad lista över de viktigaste huvudtyperna av diskontinuerliga arealer. Detta kapitel är kanske det mest intressanta i hela

boken. Då förf. i stort sett stöder sig på tidigare författare i ämnet, ger det kanske inte något fundamentalt nytt, men det bär å andra sidan en prägel av magistral överblick över hela detta vida fält av spekulationer.

Mot dessa fem första kapitel, vilka bildar den sakliga tyngdpunkten i Wulffs arbete, kan åtskilliga anmärkningar riktas. Några ha redan ovan berörts. Andra gäller framför allt litteraturbehandlingen. Bristerna evad gäller de nyare amerikanska arbetena har kommenterats av Raup i hans tillägg, varför det här inte är nödvändigt att gå in på den saken. Man är emellertid förvånad över att en klassiker som Adams icke med ett enda ord beröres. Adams gjorde redan 1902 en fundamental insats vid studiet av arealcentra i södra Alleghanybergen. De slutsatser som Adams framlade och vilka nyligen kritiskt reexaminerats av Cain, överensstämma i väsentlig grad med Wulffs egna. Också Meusel har bortglömts; genom sin »Vergleichende Arealkunde» har han lämnat viktiga bidrag till belysningen av dessa frågor med särskild hänsyn till Gamla Världens boreala delar. För en svensk växtgeograf kan det vidare synas märkligt att Hulténs »Outline of the History of Arctic and Boreal Biota during the Quarternary Period» endast i förbigående omnämnts, helst som Hulténs teori om »the equiformal progressive areas» i viss mån revolutionerat det växtgeografiska tänkandet i arealfrågor. Weimarcks principiellt viktiga arbete av 1941 »Phytogeographical Groups, Centres and Intervals within the Cape Flora» har inte alls citerats; det hade kunnat lämna väsentliga argument till Wulffs diskussion. Slutligen bör nämnas att Wulffs behandling av »the origin of areas» såtillvida är ofullständig som förf. inte medtagit de anmärkningsvärda resultat vilka under de sista årtiondena nåtts inom cytogeografi, experimentell ekologi och experimentell taxonomi. Hela problemet om arealernas ursprung är ju intimt förbundet med artbildningen i dess olika aspekter, nyligen sammanfattningsvis diskuterad av Dobzhansky, Huxley och andra.

Med undantag av slutkapitlet är hela den senare delen av boken ägnad växternas spridning och spridningsmöjligheter genom olika agens, vandringar av arter och hela floror och de kausala grundvalarna härför. Det spridningsbiologiska avsnittet är i huvudsak en icke särskilt märklig sammanställning av litteratur. Recensenten kan inte bedöma graden av fullständighet i behandlingen av denna. Heintzes stora, tyvärr ofullbordade livsverk »Handbuch der Verbreitungsökologie der Pflanzen» citeras visserligen i litteraturförteckningen, men man kan ingenstädes finna detta arbete i texten, liksom ej heller några kommentarer till det av Heintze publicerade jättematerialet.

I kapitlen »The Migration of Species and Floras and Their Causes» och »Historical Causes for the Present Structure of Areas and the Composition of Floras» rör sig förf. tydligen inom ett område där han känner sig mera hemma. Han ger här en något ofullständig men intressant och välkommenterad resumé över egna och andras forskningar. Det förstnämnda av dessa avsnitt bygger i huvudsak på Goods »migrationsteori» eller som Good själv föredrar att kalla den: »theory of tolerance». Den innebär som bekant att »a species is able to occupy only those parts of the world where the external conditions are within those of its range of tolerance. This total area which

a species can occupy in virtue of its tolerance, is conveniently termed its potential area. The size of the potential area will tend to vary with change in external conditions.» Utgående från denna teori diskuterar Wulff ämnets olika aspekter med särskild tonvikt på klimatförändringarna under tertiär och kvartär och deras inflytande på växternas vandringar i större eller mindre skala. Raup beklagar i sitt tillägg att förf. inte haft större möjlighet att ta hänsyn till den ytterst omfattande amerikanska litteraturen på detta område och särskilt då Fernalds klassiska arbeten. Med lika stor rätt kan man beklaga att Wulff av olika skäl inte kunnat inarbeta ett antal europeiska arbeten av den största betydelse i sin text. Detta gäller t. ex. Nannfeldts, Nordhagens och Selanders studier över den skandinaviska fjällflorans historiska växtgeografi, Hulténs ovannämnda arbete (som säkert hade medfört vissa förändringar i Wulffs text), Riklis utredningar i »Pflanzenwelt der Mittelmeerländer», de forskningar över bergsflororna i Nordvästafrika vilka utförts av Maire och hans lärjungar, Du Rietz' studie över de bipolära växterna, van Steenis' undersökningar över bergsflorornas vandringar i Malaysia, etc. Eftersom ett särskilt litet summariskt avsnitt behandlar parallellism mellan växt- och djurarealer, tycker man kanske dessutom att några av de allra viktigaste nyare djurgeografiska resultaten fått komma med på en kant. Något ur Mayrs och Renschs produktion borde åtminstone ha medtagits.

I likhet med Irmscher, Herzog och andra är Wulff en övertygad wegenerian. Det är kanske därför bara naturligt att hans framställning av de historiska orsakerna till florornas recenta sammansättning i huvudsak har blivit en plaidoyer för kontinentalförskjutningsteorien. En betydande del av texten har tagits i anspråk för att tillbakavisa den av Du Rietz riktade kritiken mot Wegeners teori i uppsatsen om tvenne nya *Euphrasia*-arter från Filippinerna (Sv. Bot. Tidskr. 1931). Wulff anser Du Rietz' argument bland de ur botanisk synpunkt delvis mest vägande som riktats mot den Wegenerska lärobyggnaden och försöker att motbevisa dem bl. a. på grundval av Sewards synpunkter av 1934. Att hela frågekomplexet om kontinentalförskjutningens vara eller icke vara ännu inte helt kan överblickas framgår, förutom av de hos Merrill citerade, till teorin positivt inställda geologernas arbeten (Holland 1941, Bailey Willis 1942) även av Goods helt nyligen (1950 i Nature och 1951 i the Advanc. of Sci.) publicerade sammanfattningar av frågans nuvarande läge.

Slutkapitlet innehåller en utredning av begreppet »floraelement». Wulff anser att denna term bör användas i vidaste betydelse och urskiljer med exempel fem olika huvudgrupper av dylika: geografiska, genetiska, historiska och ekologiska element samt spridningselement. Förf. avböjer de försök som gjorts exempelvis av Reichert, Eig och Wangerin att begränsa användningen av termen till en viss av dessa betydelser.

Såsom kanske framgår av ovanstående randanmärkningar ligger den största svagheten i Wulffs arbete däri att han inte haft möjligheter till en adekvat överblick över litteraturen. Värdet av Wulffs slutsatser har därför blivit mer begränsat än vad annars skulle ha varit fallet. En annan väsentlig svaghet ligger i hans reservationslösa anammande av kontinentalförskjutningsteorien. Bortsett från detta innehåller det anmälda

arbetet en sådan rikedom av fakta och synpunkter serverade i en klar och koncis form att man har anledning till stor tacksamhet mot författare och förlag att det kunnat publiceras i en västerländsk språkdräkt. WULFFS arbete eggar vid genomläsningen ibland till motsägelser och man känner sig ofta frestad att sätta frågetecken i marginalen. Kanske inte minst härigenom har »An Introduction to Historical Plant Geography» blivit en sällsynt stimulerande resumé över ett aktuellt forskningsområde.

Henning Horn af Rantzien.

GUNDERSEN, ALFRED, Families of Dicotyledons. — Waltham, Mass. (: The Chronica Botanica Co.; Uppsala: A. B. Lundequistska Bokhandeln) 1950. 237 pp. Talr. figs. Pris $ 4.50.

Den amerikanske systematikern GUNDERSEN har i en nyligen publicerad handbok över dikotyledonernas systematik och klassificering framlagt åtskilliga ändringar av tidigare system och presenterat synpunkter vilka delvis avvika från andra forskares. Det kan inte bli tal om att kritiskt väga eller ens redogöra för alla dessa ändringsförslag. Här kan endast en ytterligt schematisk sammanfattning lämnas; i övrigt hänvisas till ett närmare studium av denna, trots det lilla formatet, synnerligen innehållsrika bok.

GUNDERSENS arbete är indelat i fyra huvudavsnitt, av vilka det fjärde, som upptar lejonparten av utrymmet, innehåller en kortfattad redogörelse för det nya systemet.

Inledningsvis har förf., med hjälp av ett antal specialister, på 22 sidor lyckats inrymma några starkt koncentrerade kapitel vilka ägnats vissa grundläggande aspekter av dikotyledonernas morfologi ur systematisk synpunkt. Här skriver CH. A. ARNOLD om de fossila dikotyledonerna och O. TIPPO om vedanatomi, TH. JUST beskriver karpeller och fröämnen, H. F. COPELAND embryot, J. H. TAYLOR behandlar cytotaxonomi och W. H. CAMP slutligen växtgeografi. Av de skilda uppsatserna är särskilt TIPPOS sammanställning av de nyaste vedanatomisk-systematiska forskningarna ytterligt värdefull; resultaten inom detta i livaktig utveckling stadda forskningsområde har tydligen starkt påverkat GUNDERSEN vid hans ställningstaganden i olika systematiska frågor.

Arbetets andra del, liksom de följande skriven av GUNDERSEN själv, ger en kortfattad skildring av primitiva och avledda morfologiska karaktärer. Den tredje delen behandlar dikotyledonernas klassificering ur historisk synpunkt från LOBELIUS och BAUHIN fram till RENDLE, HUTCHINSON, BURTT-DAVY och SKOTTSBERG. En tabellarisk jämförelse mellan det av SKOTTSBERG använda systemet och systematiken i GUNDERSENS eget arbete avslutar detta tredje avsnitt.

I den fjärde, speciella delen, uppräknar GUNDERSEN 240 familjer, grupperade på 42 ordningar och 10 ordningsgrupper. *En* huvudlinje i GUNDERSENS klassificering är att systemet inledes med Polycarpicae, medan monochlamydéerna placeras högre upp i systemet såsom avledda typer. Detta är ju i enlighet med bl. a. av BENTHAM och HOOKER förfäktade synpunkter. En annan huvudlinje är att den gamla indelningen i choripetaler och sympetaler frångåtts som en konsekvens av den numera rådande upp-

fattningen att dessa grupper icke är naturliga. De har upplösts i ordningsgrupper och ordningar, ofta sammansatta av både sympetaler och choripetaler. Det är sannolikt att GUNDERSENS arbete kommer att väcka en lika livlig diskussion bland systematici som en gång kom HUTCHINSONS bekanta »kätterska» dikotyledon-klassificering av 1926 till del.

Systemet inledes alltså med ordningsgruppen *Magnolifoliae*, som omfattar dels den gamla ordningen Polycarpicae, här indelad i tvenne ordningar, Magnoliales och Ranales (: *Ranunculaceae*, *Ceratophyllaceae*, *Berberidaceae*, *Lardizabalaceae*, *Menispermaceae*) och dels Piperales. — Som tvåa följer *Cistiiflorae*, sammansatt av ordningar från olika håll: Cactales, Cistales (d. v. s. Parietales p. p.), Salicales, Papaverales (= Rhoeadales), Sarraceniales (inkl. Nepenthales), Aristolochiales (: *Aristolochiaceae*, *Rafflesiaceae*, *Hydnoraceae*) och Tamaricales (: *Tamaricaceae*, *Frankeniaceae*, *Elatinaceae*, *Fouquieraceae*). — Närmast i ordningen är nu »*Thea-gruppen*» innefattande de choripetala Thealesfamiljerna från *Dilleniaceae* till *Guttiferae* samt de sympetala Ebenales och Ericales. — *Rosaeflorae* omfattar de fyra ordningarna Rosales (tidigare till Rosales förda familjer med fria karpeller och föga eller intet endosperm; hit föres bl. a. även den tidigare i närheten av Sarraceniales ställda fam. *Cephalotaceae*), Hamamelidales (huvudsakligen tidigare Rosales-familjer med förenade karpeller och mest med ett litet embryo omgivet av rikligt endosperm: *Stachyuraceae*, *Hamamelidaceae*, *Myrothamnaceae*, *Bruniaceae*, *Cunoniaceae*, *Pittosporaceae*, *Byblidaceae*, *Hydrangeaceae*, *Saxifragaceae*, *Podostemaceae*, *Hydrostachyaceae;* här inkluderas alltså de båda tidigare ordningarna Podostemales och Hydrostachyales) samt vidare Thymelaeales (*Penaeaceae*, *Oliniaceae*, *Thymelaeaceae*, *Elaeagnaceae*) och Myrtales. — Som femte ordningsgrupp kommer nu den största delen av de gamla monochlamydéerna, förenade till den s. k. »*Ulmus-gruppen*». Hit föres Proteales (med någon tvekan), Santalales (inkl. Balanophorales), Urticales, Balanopsidales, Fagales, Leitneriales, och Casuarinales (= Verticillatae; föres hit endast med tvekan) medan Salicales, Garryales, Myricales, Juglandales, Julianales och Batidales utplanterats på andra håll i systemet. — Den sjätte ordningsgruppen omfattar Malvales (en stor del av de tidigare Columniferae-familjerna) samt Euphorbiales (: *Dichapetalaceae*, *Euphorbiaceae*, *Buxaceae;* men exkl. de tidigare oftast hit förda callitrichacéerna). — »*Geranium-gruppen*» motsvarar med vissa förändringar de tidigare ordningarna Gruinales, Therebinthales, Polygalales, Sapindales, Celastrales och Rhamnales. GUNDERSEN anför under sin »Geranium-grupp» ordningarna Rutales (*Rutaceae* och närstående familjer jämte *Julianaceae!*), Juglandales (*Rhoipteleaceae*, *Juglandaceae*, *Myricaceae*), Sapindales (inkl. Polygalales), Celastrales (inkl. Rhamnales), och Geraniales (i denna ordning innefattas även fam. *Limnanthaceae*). — Den åttonde ordningsgruppen, *Dianthiflorae*, omfattar fyra ordningar från synnerligen olika håll i de tidigare systemen: Caryophyllales (d. v. s. den största delen av centrospermerna samt den tidigare ordningen Batidales), Polygonales, Primulales (innefattar även Plumbaginales) samt Plantaginales. — Ordningsgruppen *Jasminiflorae* motsvarar schematiskt sett Tubiflorae, Ligustrales och Campanulatae i de

tidigare systemen, ehuru talrika förändringar inom gruppen har vidtagits. Fyra ordningar föras hit av GUNDERSEN: Loganiales (: *Oleaceae, Loganiaceae, Gentianaceae, Apocynaceae, Asclepiadaceae*), Polemoniales till största delen omfattande Tubiflorae-familjer), Boraginales (*Boraginaceae, Verbenaceae, Myoporaceae, Labiatae;* som sista familj möter man här med någon överraskning *Callitrichaceae*) samt Campanales (*Campanulaceae, Goodeniaceae, Stylidiaceae*). — Den tionde och sista ordningsgruppen, *Rubiflorae*, omfattar ordningarna Umbellales (*Araliaceae, Umbelliferae, Cornaceae* samt *Garryaceae*), Rubiales och Asterales (= Synandrae).

GUNDERSENS handbok avslutas med några sammanfattande anmärkningar där förf. bl. a. gör sig till talesman för utarbetandet av en standardiserad internationell förteckning över fanerogamernas familjer, samt vidare med en kort litteraturförteckning, som delvis kompletterar TURRILLS lista över taxonomiska och fylogenetiska arbeten i Bot. Rev. 8 (1942). Flertalet citerade arbeten härstammar från tiden efter 1925.

Henning Horn av Rantzien.

CORRELL, S. DONOVAN, Native Orchids of North America. — Waltham, Mass. (: The Chronica Botanica Co.; Uppsala: A. B. Lundequistska Bokhandeln) 1950. 399 pp., 164 pl. Pris $ 7.50.

SUMMERHAYES, V. S., Wild Orchids of Britain. — The New Naturalist Series. Collins, London 1951. 366 pp., 48 pl. i färg, 24 pl. i svart och vitt, 43 kartor. Pris 21 s.

Få människor torde stå likgiltiga inför en blommande orkidé och få grupper av växter torde från början ha tilldragit sig en sådan uppmärksamhet som denna stora familj. Den fackliga och populärvetenskapliga litteraturen om orkidéer är överväldigande, men deras invecklade systematik, vida utbredning och varierande, men för varje art starkt specialiserade livsfordringar gör att kännedomen om dem fortfarande ur många synpunkter är ytterst ofullständig. En stor fördel med det allmänna intresset för orkidéer är att även rent vetenskapliga arbeten över denna familj ofta finner en stor och tacksam publik utanför fackmännens krets. Ett typiskt exempel på detta förhållande utgör den första av de här anmälda böckerna.

CORRELLS arbete torde vara en av de vackraste och mest påkostade böcker som utgivits av Chronica Botanica-förlaget. Vilket inte vill säga så litet! Den är upplagd som en monografi över de inhemska orkidéerna på den amerikanska kontinenten från Aleuterna, Alaska och Hudsonviken i norr till Rio Grande och Florida Keys i söder. En införd och naturaliserad art har även medtagits: vår *Epipactis helleborine*, som på amerikansk botten för första gången påträffades 1879 vid Syracuse, N. Y., och som senare spritt sig betydligt. Arbetet är försett med utförliga bestämningstabeller. För varje art uppräknas synonymer, typlokal och typkollektion. Vidare ges en utförlig beskrivning, en koncentrerad resumé av den amerikanska utbredningen samt noggranna ståndortsupplysningar. De detaljerade uppgifter om odlingsbetingelser som för varje art lämnats av E. T. WHERRY (markorkidéer) och J. V. WATKINS (epifyter) torde vara av det största intresse för orkidéodlare. Icke mindre än 146 planscher och talrika andra

illustrationer ha utförts speciellt för denna bok av Blanche Ames Ames och Gordon W. Dillon. Var och en av bilderna är ett konstverk och samtidigt detaljerat botaniskt illustrationsmaterial av hög klass.

En anmärkning, som kan riktas mot denna annars synnerligen användbara handbok gäller det kollektiva artbegreppet. Detta framgår t. ex. inte minst vid en jämförelse med den senaste upplagan av »Gray's Manual». Författaren uppräknar för den nordamerikanska kontinenten endast 146 arter medan amerikanska florister annars brukar taxera detta antal till närmare 200. Flertalet av de »varieties» som upptas av Correll behandlas oftast såsom arter. Det ovan sagda gäller mest de nordligare arterna; beträffande de stora tropiska och subtropiska grupperna (*Epidendrum*, *Oncidium*, m. fl.) följer förf. i allmänhet den av Oakes Ames tidigare använda artbegränsningen; Ames hann också läsa igenom delar av manuskriptet före sin död. — Av särskilt växtgeografiskt intresse är några tropiska arter, vilka påträffats i Florida efter 1933, och som alltså inte medtagits i Smalls »Manual of the Southeastern Flora».

Vi har blivit bortskämda med arbeten av verkligt hög klass i »New Naturalist» serien. Det senaste tillskottet till denna, Summerhayes' arbete om Britanniens orkidéer, utgör intet undantag. Denna bok skiljer sig ur vissa synpunkter från sin ovan anmälda amerikanska motsvarighet. Sålunda ger den jämförelsevis utförliga och synnerligen fängslande framställningar av vissa drag i orkidéernas biologi, deras groningsstadier, förbindelse med mycorrhiza-svampar, senare utveckling, saprofytism, och vegetativa fortplantning. Ett särskilt kapitel är ägnat orkidéblommans byggnad, och i andra mästerliga avsnitt får man följa orkidéernas pollinering, befruktning och postflorala stadier. Huvudparten av bokens innehåll ägnas emellertid åt en detaljerad redogörelse för de mer än 50 arter (därav ett tiotal *Dactylorchis*-former) som påträffats på de brittiska öarna. Samtliga arter (utom *Orchis cruenta* och *O. occidentalis*) ha illustrerats genom vackra och karakteristiska färgfotografier. Då flertalet (31) av de brittiska arterna (här frånräknat det delvis outredda *Dactylorchis*-komplexet) även påträffats inom vårt floraområde, torde detta arbete vara av stort intresse även för nordiska florister.

Henning Horn af Rantzien.

Vegetationskarte der Schweiz, herausgegeben von der Pflanzengeographischen Kommission der Schweizerischen Naturforschenden Gesellschaft. Aufnahmen und Bearbeitung von Emil Schmid. Masstab 1:200 000. Blätter 1—4. — Hans Huber, Bern, 1949 –51. Pris per blad (papper) 12 schwfr.; (linneväv) 16 schwfr.

Det är en imponerande prestation, i sitt slag troligen enastående, som schweizarna utfört med det växtgeografiska karteringsarbete vars resultat nu föreligger komplett i form av fyra stora kartblad. En växtsociologisk detaljkartering av ett land som Schweiz torde inte minst ha bjudit på avsevärda tekniska svårigheter vid den kartografiska redovisningen av materialet. På grund av landets topografiska brutenhet och dess geografiska läge som ett övergångsområde å ena sidan mellan Centraleuropas bokskogsregion och Mediterranis, å den andra mellan det oceaniska Västeuropa och

det kontinentala Österuropa, finns ett mycket stort antal associationer av olika växtgeografisk karaktär representerade, sannolikt flera än 80. Då alla dessa associationer växlar på en mycket begränsad yta, är det av ett betydande metodologiskt intresse att se på vilket sätt man i detta fall har lyckats genomföra kryssningen mellan Scylla och Charybdis: för långt driven schematisering eller bristande överskådlighet.

Det kan genast sägas att man lyckats undvika undervattensklipporna kring Scylla, alltför schematiserade kan ingen kalla dessa kartblad. Grundtanken vid planerandet av dem har varit att man så vitt möjligt sökt utmärka utbredningen av varje association. I vissa fall har detta icke varit möjligt, så när det gällt vissa stäppsamhällen (*Stipa*-stepperna, Festucetum glaucae, etc.), *Quercus-Tilia-Acer*-skogarna samt Pineta silvestris, där man delvis fått röra sig med mer kollektiva enheter. Associationerna har i teckenförklaringen grupperats i enheter av hög rang, dels allianser, dels ännu mer omfattande begrepp. Varje sådan enhet av hög rang har på kartorna inlagts med en viss färg. Så har t. ex. de associationer som sammanförts under *Larix europaea - Pinus cembra* - skogarna s. lat. utmärkts med en gråblå färg. Associationerna inom samma enhet hållas i sär genom att vissa symboliska tecken i svart inritats på grundfärgen. Så har den i lärk-cembratall-skogarna ingående associationen Alnetum viridis utmärkts genom symbolen U. De delar av den överordnade enheten som f. n. intagas av kulturlandskap av olika slag (åker, betesmark, vinberg etc.), men som under naturliga förhållanden skulle ha varit bevuxna med phytocoenoser tillhörande denna grupp har utmärkts genom runda fläckar i den karakteriserande grundfärgen mot vit botten. Utanför associationsramen förekommer slutligen en rent floristisk kartering av ett tjugotal växtgeografiskt särskilt viktiga arter (*Hippophae*, *Acer pseudoplatanus*, *Juniperus sabina*, m. fl.), vilkas förekomst utmärkts genom särskilda tecken.

Genom det överväldigande faktamaterial som sålunda inarbetats på kartbladen är dessa delvis tämligen svårlästa. Detta gäller kanske speciellt för Wallis, Tessin och Graubünden, där på grund av det starka inslaget av submediterrana typer, inskjutna i montana och alpina element, associationerna alldeles särskilt trängs med varandra. Genom det lyckade greppet med olika grundfärg för överordnade enheter får man dock en rätt klar bild av dessas väsentliga utbredning, även om detaljerna i associationernas förekomst helst bör avnjutas med hjälp av förstoringsglas.

En slutsats kan man kanske dra ur dessa kartblad: växtsociologiskt torde de schweiziska botanisterna känna varje kvadratmeter av sitt land. Och ingen botaniskt intresserad person som ämnar styra kosan till detta paradis för sällsynta växter borde försumma att förutom turistkartor och Reiseführer medta ett exemplar av »Vegetationskarte der Schweiz».

Henning Horn af Rantzien.

Geitler, Lothar, Schnellmethoden der Kern- und Chromosomenuntersuchung. 3. Aufl. — Springer-Verlag, Wien, 1949. 35 pp. Pris $ 1.50.

Geitlers lilla skrift om snabbmetoder för karyologiska och cytologiska undersökningar rönte, då den först utkom (1939) ett stort intresse. Arbetet

har i flera år varit utgånget från förlaget och föreligger nu i en tredje utökad och något omarbetad upplaga. Avbildningarnas antal har ökats från 8 till 13, och i övrigt föreligger en del tillägg i texten. GEITLER beskriver i detalj de tre allmänt använda snabbmetoderna: karminättiksyremetoden, osmiumtetraoxidmetoden och slutligen den av HEITZ införda metod som bygger på FEULGENS nuklealreaktion. Ett slutkapitel behandlar lämpliga zoologiska och botaniska undersökningsobjekt.

Henning Horn af Rantzien.

COWAN, JOHN MACQUEEN, The Rhododendron Leaf. A Study of the Epidermal Appendages. — Oliver & Boyd, Edinburgh & London, 1950. 120 pp., 18 pl. Pris 21 s.

Det har länge varit känt att indumentbeklädnaden på undersidan av *Rhododendron*-arternas blad lämnar värdefulla karaktärer för den taxonomiska klassificeringen inom detta kritiska släkte. Detta påpekades först av JULIEN VESQUE 1885 och har sedan spelat en allt viktigare roll i litteraturen fram till den monumentala monografien »Species of Rhododendron» utgiven 1930 av The Rhododendron Society. Någon större jämförande granskning av bladundersidans trichom har dock aldrig företagits.

J. M. COWAN, auktoritet på släktets systematik och anställd vid de internationellt ryktbara *Rhododendron*-odlingarna i Royal Botanic Garden of Edinburgh har nu med en intressant och typografiskt synnerligen tilltalande volym utfyllt denna lucka i vårt vetande. Man får tyvärr inga upplysningar om hur många av de betydligt mer än 200 arterna som studerats av förf. (betydligt mer än hälften av artantalet citeras emellertid i texten), däremot framgår det tydligt att de undersökta arterna representera släktets alla undergrupper. COWAN har företagit en morfologisk klassificering av de olika indumenttyperna, först en grundläggande dylik i papiller, hår och fjäll, varefter dessa tre huvudkategorier vardera indelats i ett stort antal undertyper. Denna morfologiska gruppering har vidare korrelerats till den taxonomiska indelningen av släktet (enligt »Species of Rhododendron»). Särskilt instruktiv är i detta avseende den tabell som utvisar fördelningen av de olika typerna av papiller, hår och fjäll på undersläkten, sektioner och andra infrageneriska grupper. Illustrationsmaterialet är utomordentligt vackert och omfattar både teckningar och ett antal färgfotografier av bladens dorsalsida. Förf. betonar särskilt att en jämförelse mellan indumentets byggnad hos olika arter måste ske inom ett bestämt område på undersidan av likåldriga, icke för unga blad, en regel mot vilken tidigare har syndats. Andra avsnitt i denna monografi över de epidermala utskotten hos *Rhododendron* behandlar dessas allmänna byggnad och fylogeni, deras utveckling och betydelse för den levande växten.

Henning Horn af Rantzien.

NOTISER.

Doktorsdisputationer. För vinnande av filosofie doktorsgrad försvarade fil. lic. Gunnar Östergren den 10 mars 1951 vid universitetet i Lund en avhandling »The Mechanism of Co-Orientation in Bivalents and Multivalents»; fil. lic. Hemming Virgin den 12 maj 1951 vid Stockholms högskola »The Effect of Light on the Protoplasmatic Viscosity»; fil. lic. Gunnar Harling den 16 maj 1951 vid Stockholms högskola »Embryological Studies in the Compositae I—III»; fil. lic. Visvaldis Slankis den 25 maj 1951 vid universitetet i Uppsala »Über den Einfluss von β-Indolylessigsäure und anderen Wuchsstoffen auf das Wachstum von Kiefernwurzeln. 1»; fil. lic. Magnus Fries den 26 maj 1951 vid universitetet i Uppsala »Pollenanalytiska vittnesbörd om senkvartär vegetationsutveckling, särskilt skogshistoria, i nordvästra Götaland»; och fil. lic. G. Lindstedt den 26 maj 1951 vid Stockholms högskola en avhandling »Constituents of Pine Heartwood».

Lunds universitet. Fil. dr Sigvard Lillieroth har förordnats till docent i limnologi; fil. dr Gunnar Östergren till docent i ärftlighetslära; fil. dr Hemming Virgin till docent i botanik.

Riksmuseets paleobotaniska avdelning. Till professor och föreståndare för avdelningen har från den 1 juli 1951 utnämnts museiassistenten, docent Olof H. Selling.

Den ledigförklarade museiassistentbefattningen vid avdelningen hade vid ansökningstidens slut sökts av fil. lic. Britta Lundblad, Stockholm, och fil. dr Herman Persson, Stockholm.

Uppsala universitet. Fil. dr Birgitta Norkrans har förordnats till docent i botanik; fil. dr Magnus Fries till docent i växtbiologi.

Stockholms högskola. Fil. dr Gunnar Harling har förordnats till docent i botanik.

Upprop.

Insamling av Collybia velutipes, vinternagelskivling.

För en pågående undersökning önskas färskt material i så stor utsträckning som möjligt av vinternagelskivlingen, *Collybia velutipes*. Under hösten och vintern önskas material från skilda delar av landet insänt till Institutionen för fysiologisk botanik, Uppsala, för fil. mag. Karin Aschans räkning, som hoppas på välvilligt bistånd av landets botanister.

Materialet kan lämpligen sändas som prov utan värde. Från varje växtplats behövs bara en eller ett par fruktkroppar. Insändes samtidigt material från olika lokaler, är det viktigt att fruktkropparna förpackas väl skilda. Insamlat material torde ha anteckningar om geografiska växtplatsen, insamlarens namn och adress och helst även anteckning om vad för trädslag svampen vuxit på (medsänd helst ett prov av trädslaget) och om fruktkropparna i fråga vuxit på levande träd eller gamla stubbar och om förekomsten på ifrågavarande lokal är riklig.

Särskilt gärna önskas abnorma fruktkroppstyper och om möjligt även exemplar från barrträd, vilket är ytterst sällsynt.

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THERMOTROPIC CURVATURES IN THE AVENA COLEOPTILE.

BY

CARL ERMAN.

Introduction.

The thermotropic curvatures belong to one of the least studied branches of irritation physiology, and literature is consequently very scarce on this subject.

The concept of thermotropism was introduced into the scientific nomenclature by VAN TIEGHEM (1874). He tried to explain the thermotropic curvatures without support of experimental investigation. Thus, he considered that, if the one side of a plant is exposed to a more favourable temperature than the opposite one, the former will grow more quickly than the latter, and the result will be that the plant curves away from the most favoured side. At temperatures below the growth optimum of the plant a negative curvature away from the source of heat always appears, at temperatures above the optimum, on the contrary, towards it.

Already WORTMANN (1883), however, could experimentally demonstrate that thermotropism was a phenomenon of a far more complicated nature than VAN TIEGHEM had imagined. He used germinal shoots of *Ervum lens*, *Pisum sativum*, *Zea mays*, and *Phaseolus multiflorus* and the plants had been grown in zinc boxes with moist sawdust. By unilateral heating with gas-jets a temperature fall of 4 to 7.6° C. a centimeter was attained. At temperatures higher than the limit temperature characteristic of each species W. always obtained negative curvatures; at lower temperatures, on the other hand, they were positive. Just at the limit temperature, again, positive as well as negative curvatures were found. This held in *Ervum*, *Pisum*, and *Zea*, while in *Phaseolus* only negative curvatures were noticeable.

Also KLERCKER (1891), who made purely quantitative measurements of the size of the curvature angles at thermotropic curvatures in the roots of *Pisum sativum* and other plants, arrived at the result that these curvatures are of a rather complex nature and to all appearances reflect the action of antagonistic factors. That makes us think of a simultaneous hydrotropic reaction.

The hitherto most detailed analysis of thermotropic curvature was produced by COLLANDER (1919). His chief experimental material consisted of *Avena* coleoptiles (the »Svalövs Seger» oats) and *Helianthus* hypocotyls.

COLLANDER puts *int. al.* the question, does the thermotropic curvature depend on radiation as such (*i.e.* without transformation of radiation energy into thermic energy) or is it caused by the unilateral warming-up? In the latter case a transpiration rise might also be imagined to be the primary cause.

In his experiments he measures the curvature angles either in a given time or at 30 min. intervals. It is evidently impossible in this manner to obtain a really detailed picture of the development of curvatures. In the investigation described below I have therefore chosen reading intervals as short as 5 min., *i.e.* the same interval as that used in the study of the thermogrowth reaction. In this way the conditions are also more favourable for a direct study of a possible connection between these two reactions.

Experimental arrangement.

All the experiments were carried out on detached specimens placed in the spacious dark room, which was provided with ventilation devices. The coleoptiles were raised under permanent red light in the disconnected thermostat (the thermostat has earlier been employed in my investigation on the thermogrowth reactions, ERMAN 1951), in which consequently the same temperature prevailed as in the experimental room. At least 24 hours before the beginning of the experiment they were placed in the said room, where a permanent red reading-light was also burning. Fig. 1 shows the arrangement of the apparatus.

The preparation tubes with the material (B) were placed on a Petri dish (D) 3 cm high and 19 cm in diameter. The dish was filled with water. On a line with the phototropically inactive darkroom lamp (A) but on the opposite side of the specimen selected

Fig. 1. Arrangement of the apparatus in thermotropic curvature experiments (see explanation in text).

for study was the horizontal microscope placed, and at right angles to its optical axis a 10 cm »Glory» radiator for ultrared rays (C). This was screened from the specimen by a thin, concave, metallic reflector. It was made sure by means of blind tests that the unilateral heating by the radiator did not cause any displacement in the optical system.

The coleoptiles were always orientated in a profile position in relation to the microscope, and the reading was carried out by the aid of a horizontal ocular-micrometer scale. Accordingly, the reading values do not directly indicate the angular deflections of the coleoptile but the displacement of the coleoptile apex in relation to a relative zero value. To read these deflections exactly by the 1/10 divisional line, presented a certain amount of technical difficulty, wherefore the reading-values were rounded to the next higher 1/2 divisional line.

A well-grounded objection might have been raised against making the deflections of the coleoptile apex the basis of quantitative curvature measurements, if it had been a question of phototropic or geotropic curvatures. As shown already by Tröndle (1913) inter al. the curving begins in these in the apical part of the coleoptile, gradually to continue basipetally. Collander, however, found quite another state of things in thermotropic curvatures. Thus, there is no apical perception in them, the curving begins simultaneously all along the coleoptile. For 5 different zones of a coleoptile 24 mm in length he accordingly obtained (table 7, p. 30) the following curvature values, counting from the apex:

Time:	0	30	60	90 min.
Zone I	0°	8°	8°	10°
Zone II	0°	6°	7°	10°
Zone III	0°	4°	4°	5°
Zone IV	0°	3°	4°	4°
Zone V	0°	2°	1°	2°

The apical zone showed the greatest deflection for other coleoptile lengths also during the first 60 minutes after the unilateral heat-radiation had set in. Later on it may, on the other hand, be somewhat out-distanced by the middle zones. In this connection, however, it is just the first 60 minutes of the curving reaction that are of interest.

The thermotropic curvatures after a slow rise of temperature to a subsequent constant temperature.

With the coleoptiles in the above-described experimental arrangement at a distance of 12.5 cm from the source of heat and with an original room temperature of 21° C., the temperature at the place of the specimen studied will rise by 3.8° within 15 min. Then it remains constant in the course of the experiment. On account of the too small volume of the radiator, however, the temperature of the experimental room does not change.

Table I below contains the results of 5 experiments chosen at random in a series of experiments carried out under the above-mentioned conditions. The values in the table express the divergences of the coleoptile apex from a relative zero value at the beginning of the observations. A positive curvature towards the source of heat is indicated without sign, a negative one with a minus sign. The nutations of the coleoptile apices were observed for 30 min. before the radiator was connected (= ↓).

Fig. 2 presents the curvature graph obtained from the mean values for the above table.

From a relatively flat initial phase during the first 40 minutes after the onset of the irritation the curve ascends steeply to the 75 min. point, where the maximum positive curvature is attained. This lasts about 20 min., whereupon a regress sets in.

COLLANDER also found the maximum curvature falling at approximately the same point of time (between 60 and 90 min.).

As is evident from the values in table I, the value of the curvatures rises with the length of the coleoptile at the same heating. Thus, with a coleoptile length of 10 mm, the maximum divergence is about 105 dividing lines, with a length of 22 mm 165 dividing lines, finally to reach, with 34 mm, no less than 300 dividing lines (= 2400 μ).

Table I. Thermotropic curvatures in the »Svalövs Primus» oats. Rise in temperature 3.8° C.

Time	5	10	15	20	25	30
Col. length						
I. 10 mm	0	0	–5	–5	–5	–10
II. 18 mm	5	10	15	15	20	15
III. 20 mm	5	5	10	10	10	5
IV. 22 mm	0	0	5	5	5	10
V. 34 mm	5	15	15	10	10	15
Temp.	21° C	+	+	+	+	21°

Time	5	10	15	20	25	30	35	40	45
Col. length									
I.	–20	–20	–10	0	0	10	15	20	30
II.	50	50	40	40	40	35	40	40	60
III.	5	10	20	30	25	30	50	65	75
IV.	30	50	55	50	50	50	50	50	55
V.	30	50	60	70	90	100	120	120	150
Temp.	22,5°	23,7°	24.8°	24.8°	then constant				

Time	50	55	60	65	70	75	80	85	90
Col. length									
I.	45	70	85	95	95	100	105	105	105
II.	85	95	100	105	105	100	95	100	105
III.	80	85	120	120	125	125	125	125	125
IV.	75	100	125	150	165	160	160	165	155
V.	190	220	235	240	250	270	290	300	300
Temp.	constant								

Time	95	100	105	110	115	120	125	130	135 min.
Col. length									
I.	100	100	95	80	80	75			
II.	95	80	70	65	70	75	65	60	55
III.	130	125	120	110	110	105	105	105	95
IV.	140	140	125	100	105	105			
V.	300	300	285	250	230	230			
Temp.	constant								

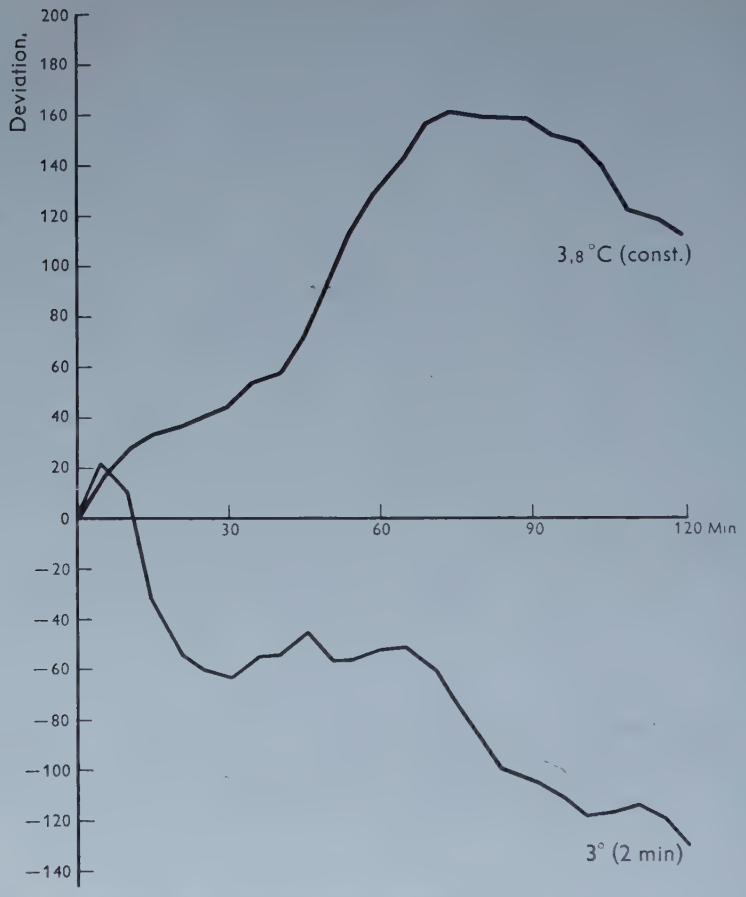

Fig. 2. The progress of the thermotropic curvatures in the *Avena* coleoptile on a short, unilateral temperature rise of 3° C. (for 2 min.) and up to a constant one by 3.8° C., respectively. The length of the coleoptiles is 35 and 38 mm respectively.

The thermotropic curvatures on short heating to various temperatures.

If the coleoptiles were placed at a distance of 7.5 cm from the radiator and this was connected for 2 min., the temperature rose at the place of the coleoptile by 3° C. within 5 min., and the initial temperature was restored after another 5 min. The curvature values obtained are given in table II.

The curves show here quite a different aspect than those in table I.

Table II. Divergences of the coleoptile apex on an abrupt and short rise of temperature by 3° C. Room temperature 21° C. ↑ = rise of temperature. Experimental material: the Svalövs Primus» oats.

Time	5	10	15	20	25	30
Col. length						
I. 23 mm	5	5	10	10	10	5
II. 32 mm	0	5	5	0	0	–10
III. 37 mm	0	0	0	–5	–10	–10
IV. 40 mm	0	0	0	15	15	20
V. 46 mm	0	–5	–5	–10	–10	–15

	5	10	15	20	25	30	35	40	45	50
I.	20	5	–20	–35	–40	–30	–25	–20	–10	–5
II.	–10	–20	–75	–100	–105	–110	–110	–105	–105	–125
III.	45	35	–30	–65	–70	–70	–50	–35	0	–20
IV.	50	25	–80	–130	–130	–105	–65	–55	–55	–70
V.	0	–10	–30	–60	–80	–120	–135	–150	–165	–175

	55	60	65	70	75	80	85	90 min.
I.	0	5	0	–20	–35	–45	–35	–25
II.	–140	–130	–115	–110	–130	–165	–190	–210
III.	–15	–15	–45	–60	–75	–95	–120	–150
IV.	–60	–45	–30	–25	–25	–25	–30	–35
V.	–180	–185	–170	–160	–180	–205	–200	–180

In fig. 2 the curvature graph based on the values of two experiments with approximately the same length also begins with a short positive initial phase which, however, immediately changes to negative values. Between 30 and 65 min. the negative curvature decreases and then increases again rapidly. The increase of the negative curvature can continue for an hour more, before any tendency to renewed curvature appears.

In the preceding curve with prolonged heating and when, accordingly, the material studied is supplied with far larger quantities of heat under a maintained intensity of radiation than at the more transitory heating in the latter series of experiments, a positive

Table III. Deviations of the coleoptile apex at a radiation time of 3 min. Rise of temperature 6° C. within 5 min. Room temperature reached again after 15 min. (= 21° C.). Experimental material: the »Svalövs Primus» oats.

Time	5	10	15	20	25	30	5	10	15	20
Col. length										
I. 14 mm	0	0	0	0	0	0	–5	–5	–15	–15
II. 18 mm	–5	10	–20	–25	–30	–40	30	–40	–45	120
III. 20 mm	5	5	5	10	10	10	40	10	–35	–50
IV. 22 mm	0	0	5	5	5	10	25	25	10	0
V. 29 mm	0	0	–5	–5	–10	–15	85	85	60	15
VI. 32 mm	–5	–10	–15	–20	–25	–30	–5	–70	–200	–215
VII. 42 mm	0	–5	–5	–5	–10	–25	30	15	–35	–85

	25	30	35	40	45	50	55	60	65	70	75
I.	–25	–25	–30	–30	–30	–20	0	20	30	35	30
II.	–140	–140	–110	–95	–95	–115	–135	–145			
III.	–55	–90	–10	20	15	0	–30	–55	–70	–70	–70
IV.	10	25	40	50	60	65	75	80			
V.	–45	–85	–105	–90	–10	65	110	120	110	95	95
VI.	–200	–120	–40	45	70	70	70	105	105	85	50
VII.	–200	–230	–235	–230	–205	–150	–110	–100	–100	–80	–90

	80	85	90	95	100	105	110	115	120	
I.	15	0	10	20	25	20	10	0	0	
II.										
III.	–90	–110	–115							
IV.										
V.	105	115	125	110	95	50	10	–5	–20	(180 min. =
VI.	5	–5	–15							–115)
VII.	–130	–170	–195	–225	–225	–225	–260	–310	–335	

curvature is obtained, in the latter case again, a negative one. This would, then, speak in favour of the theory that the quantity of heat supplied, not the radiation as such, would be responsible for the progress of the thermotropic curvature.

Collander (p. 21) also arrives at the conclusion that »the curvature is not provoked exclusively by the radiation as such, but that

Table IV. Deviations of the coleoptile apex at a radiation time of 5 min. Rise of temperature 12° C. Room temperature reached again after 20 min. (=21° C.). Experimental material: the »Svalövs Primus» oats.

Time	5	10	15	20	25	30	5	10	15	20
Col. length										
I. 18 mm	0	0	0	5	10	10	25	–5	–25	–30
II. 20 mm	5	10	10	15	15	15	25	55	65	70
III. 28 mm	–5	5	–10	–10	–10	–15	40	75	75	70
IV. 29 mm	5	20	30	35	35	30	150	140	120	85
V. 32 mm	0	0	0	0	–15	–10	170	240	90	290
VI. 33 mm	5	–15	–20	–25	–35	–45	85	165	220	240
VII. 35 mm	0	0	5	0	0	–5	120	205	260	200

	25	30	35	40	45	50	55	60	65	70	75
I.	–20	–5	10	25	35	35	25	20			
II.	70	75	70	65	55	45	45	60	80	110	155
III.	65	60	60	50	60	70	70	70	70	75	80
IV.	70	40	10	–10	20	25	–25	–25	–20	–20	–15
V.	295	270	270	285	295	295	295	295	300	320	240
VI.	235	235	235	250	280	335	390	440	460	475	495
VII.	275	275	280	295	310	315	335	345	365	390	410

	80	85	90	95	100	105	110	115	120 min.
I.									
II.	160	175	190						
III.	90	100	110	140	160	180	200	240	270 (after min. =
IV.	–5	0	30	50	70	95	125	140	150 400)
V.	350	390	400	415	445	450	455	455	460
VI.									
VII.									

the unilateral temperature rise produced by radiation is the cause of it in such wise that the attainment of a certain critical temperature is a condition of the reaction».

By keeping the distance between the heating radiator and the specimen studied (7.5 cm) but with increase of the radiation time, the curvature graphs of various rises in temperature were studied. The results are given in tables III—VI.

Table V. Deviations of the coleoptile apex at a radiation time of 10 min. Rise of temperature 20° C. Room temperature 19° C. (See temperature curve below!) — Experimental material: the »Svalövs Primus» oats.

Time	5	10	15	20	25	30	5	10	15	20
Col. length										
I. 8 mm	0	0	–5	–5	–10	–10	0	5	5	5
II. 11 mm	5	5	5	5	0	0	0	15	15	10
III. 15 mm	0	0	0	0	0	–5	15	100	110	105
IV. 15 mm	–5	–10	–20	–25	30	–35	–35	–15	0	15
V. 17 mm	0	0	0	5	5	10	30	110	145	145
VI. 22 mm	5	15	25	30	30	35	65	180	160	150
VII. 28 mm	–5	–10	5	10	10	10	110	405	370	325
VIII. 30 mm	15	25	30	35	45	50	200	470	465	420
IX. 31 mm	–5	–10	–15	–20	–25	–30	110	470	440	380
X. 33 mm	–10	–15	–20	–25	–30	–30	50	220	255	290
XI. 37 mm	–15	–20	–25	–30	–40	–50	60	400	395	406
XII. 39 mm	5	10	10	10	15	15	125	490	465	380

	25	30	35	40	45	50	55	60	65	70	75
I.	0	0	0	0	0	5	5	5			
II.	10	10	10	10	5	5	5	0			
III.	100	95	85	80	80	75	75	60			
IV.	20	25	30	40	35	35	35	40			
V.	145	145	150	155	160	160	165	165	160	160	155
VI.	150	150	150	150	160	170	170	190	195	200	210
VII.	290	260	245	235	230	225	230	230	235	235	240
VIII.	370	330	285	270	250	240	240	245	260	285	320
IX.	375	370	330	310	300	295	295	295	295	295	295
X.	300	300	300	310	310	310	315	315			
XI.	410	410	410	415	425	430	440	470	495	505	535
XII.	325	275	255	245	245	245	245	245	245	260	270

	80	85	90	95	100	105	110	115	120	125
V.	150	145	140	140	130	120	110	100	90	80
VI.	220	225	225	230	230	230	225	220	195	190
VII.	245	250	255	265	275	390	410	425	410	425
VIII.	370	420	445	450	445	425	400	380	360	345
IX.	300	300	305	310	320	335	360	385	410	445
XI.	570	590	615	640	660	690	730	750	780	830
XII.	260	270	285	295	320	360	395	440	480	535

	130	135	140	145	150	
V.	70	65	60	50	40	
VI.	180	170	160	150	140	
VII.	450	480				
VIII.	345	320	300	275	255	(after 240 min.=180)
IX.	485	530	625	665	690	(after 180 min.=860)
XI.	950	980				
XII.	540	540	540	540	525	(after 240 min.=150)

The temperature curve for table V was as follows:

19° ↓ 31° 38° ↑ 27° 23.5° 21° 19° constant

Finally, the experimental series given in table VI overleaf, with a rise of temperature 20° C. to 42° C., *i.e.* by a total of 22°, was carried out. In this table also the specimens studied are arranged acc. to length. The temperature curve in this series of experiments was as follows:

20° ↓ 32° 40° 42° ↑ 31° 26° 24.5° 23° 22° 21° 20° constant

To plot the curvatures for the respective rises of temperature on the basis of the mean values of the above tables is impossible, as several of the experiments, on the one hand, were followed for only 60 min. after the heating had set in, and the average length of the coleoptiles, on the other, varies widely while the curvature values obviously as a rule increase with rising length of coleoptile. (This varies in tables I—VI between 6 and 46 mm.) I have therefore instead selected coleoptiles of approximately the same length (about 30 mm) and constructed diagrams on the basis of their curvature values (see fig. 3).

On examination of the separate curves in fig. 3, it will be found that all of them except that corresponding to the values in table II, Col. II. (the other coleoptiles in this table, however, show at first positive curvature values) have a distinct initial phase, the duration of which approximately coincides with the ascending branch of the curve for temperature rise. Then follows a regression phase which leads to a recurvature. In the curve for the temperature rise by 3° C. the latter turns into a gradually increasing negative curvature, which remains for 2—3 hrs. before a recurvature begins to appear.

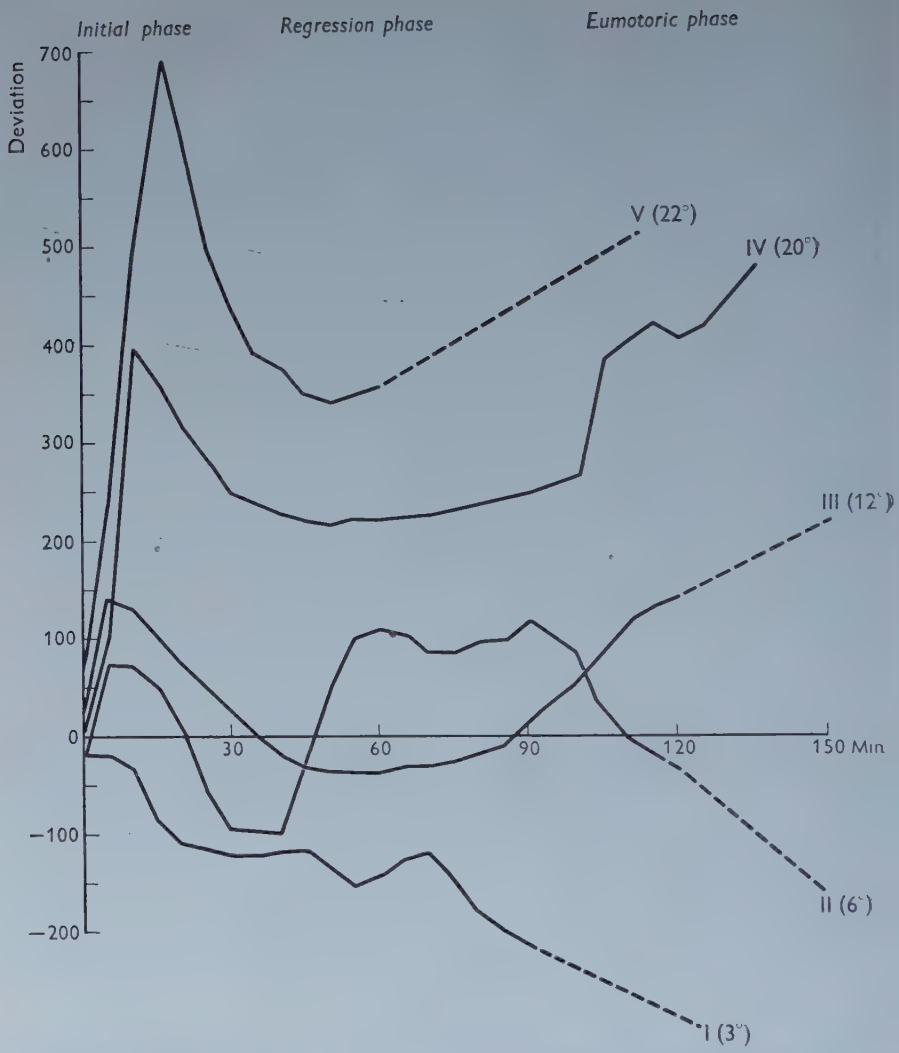

Fig. 3. The development of the thermotropic curvatures in *Avena* coleoptiles (the »Svalövs Primus» oats) at unilateral heat radiation. Coleoptiles of the length of about 30 mm.

In curve II, *i.e.* at a temperature rise of 6° C., a eumotoric phase that turns the curve into a positive direction succeeds to a regression phase, which results in a transient negative curvature. At the 90-min. point a regression begins that ends in a definitive negative curvature (after 180 min.).

For the 3° curve as well as for the 6° curve the final issue will accordingly be a negative curvature.

Table VI. Deviations of the coleoptile apex at a radiation time of 15 min. Rise of temperature 22° C. within 15 min. Room temperature (= 20° C.) reached again after 50 min. — Experimental material: the »Svalövs Primus» oats.

Time	5	10	15	20	25	30	5	10	15	20
Col. length										
I. 6 mm	0	–5	–10	–10	0	0	0	10	0	0
II. 8 mm	5	5	10	10	10	10	10	10	10	15
III. 9 mm	–5	–5	–10	–10	–15	–10	–10	20	50	50
IV. 10 mm	0	5	10	10	10	5	10	20	30	30
V. 11 mm	5	10	10	15	15	20	20	25	30	20
VI. 11 mm	0	0	5	5	10	10	10	20	35	40
VII. 12 mm	0	–5	–15	–15	–20	–20	–20	–10	5	10
VIII. 14 mm	0	–5	–10	–15	–15	–20	10	30	60	50
IX. 14 mm	5	10	15	15	15	15	25	60	100	85
X. 15 mm	0	0	0	–5	0	5	30	85	140	140
XI. 16 mm	5	20	20	25	20	10	30	65	110	105
XII. 18 mm	5	10	25	30	35	35	75	165	250	245
XIII. 20 mm	0	–5	–10	–5	–5	0	60	150	220	185
XIV. 21 mm	0	–5	–10	–15	–20	–10	40	120	200	195
XV. 22 mm	10	15	15	20	25	25	55	135	190	180
XVI. 24 mm	10	25	30	30	15	0	20	120	260	230
XVII. 25 mm	–5	–5	–5	0	5	10	10	30	85	95
XVIII. 25 mm	5	10	20	20	20	20	75	270	480	470
XIX. 25 mm	15	25	30	40	40	35	125	400	550	475
XX. 28 mm	0	10	30	50	70	90	250	500	700	605
XXI. 29 mm	0	–5	–5	0	5	10	145	450	620	585
XXII. 40 mm	0	10	5	–20	–35	–30	150	480	790	710

	25	30	35	40	45	50	55	60	65	70	75	80
I.	0	0	0	0	–5	–10	–5	0				
II.	10	15	15	25	30	30	25	20				
III.	50	45	45	45	40	40	40	40				
IV.	25	25	20	15	15	15	10	10				
V.	5	0	0	–5	–10	5	40	55	60	65	65	65
VI.	40	30	30	30	35	45	60	75	90	110	120	130
VII.	0	–10	–15	–15	–15	–15	–20	–20	–5	0	5	15
VIII.	40	40	35	30	30	25	25	20				
IX.	75	65	65	60	55	55	55	55	60	80	80	95
X.	130	125	125	125	120	120	115	110				
XI.	105	105	110	115	120	120	125	125				
XII.	245	250	255	255	250	250	250	255	260	265	265	270

Time	25	30	35	40	45	50	55	60	65	70	75	80
XIII.	180	180	170	170	170	180	185	185				
XIV.	195	195	190	180	180	180	180	180				
XV.	150	145	125	120	115	115	105	100	105	105	95	95
XVI.	175	170	170	170	180	190	200	210	210	215	215	220
XVII.	110	120	140	145	155	160	170	175	180	180	190	195
XVIII.	430	405	395	380	375	375	370	370				
XIX.	390	330	320	295	290	285	285	280				
XX.	500	445	400	385	360	350	360	365	(after 110 min. = 515)			
XXI.	530	460	430	400	370	350	330	325	320	320	326	325
XXII.	685	640	595	575	575	555	530	510	515	510	510	540

	85	90	95	100	105	110	115	120	
VII.	40	80	115	140	170	180	195	210	(after 240 min. = 190)
IX.	110	125	135	145	150	160	165	165	
XII.	270	275	275	280	285	295	305	320	
XVI.	225	230	235	240	245	250	260	270	
XVII.	200	205	210	215	220	225	230	230	
XXII.	565	575	600	635	670	740	800	845	(after 180 min. = 1125)

At the temperature rises by 12°, 20°, and 22° respectively, we find a more and more distinct initial phase. Here also it is succeeded by a regression phase and finally by a eumotoric one. The latter, however, always results in a lasting positive curvature, which is directed towards the source of heat and can, with small oscillations, remain as long as 3 to 4 hrs. before it visibly decreases.

The curvature of the initial phase and the temperature curve run close together. This is seen from fig. 4, in which the temperature curve was read at intervals of one minute. The eumotoric curvature, on the other hand, does not begin until the temperature is restored to constant room temperature (fig. 5).

Thus, the thermotropic curvature graph obtained on a unilateral heat radiation seems to be composed of

I. a positive initial phase,
II. a successive regression phase, and
III. a eumotoric phase, which leads to a negative curvature at less considerable temperature rises, and to a positive curvature at more considerable ones.

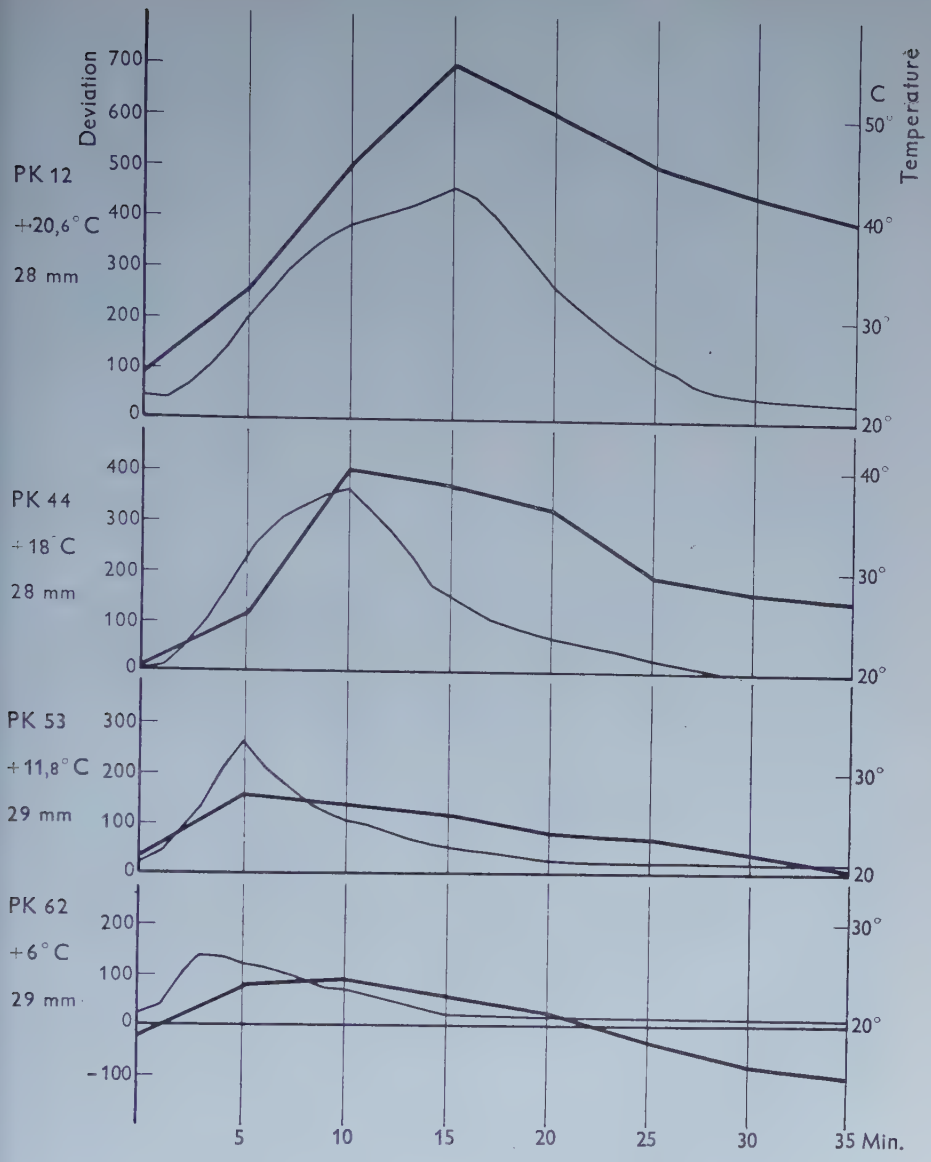

Fig. 4. Curvatures of the initial phase and curves of temperature at thermotropic curvatures in coleoptiles of *Avena sativa*.

Accordingly, different curvature regions would exist for the thermotropic curvatures in conformity with what Aritz (1915), Du Buy and Nuernbergk (1929), and others showed for the photo-

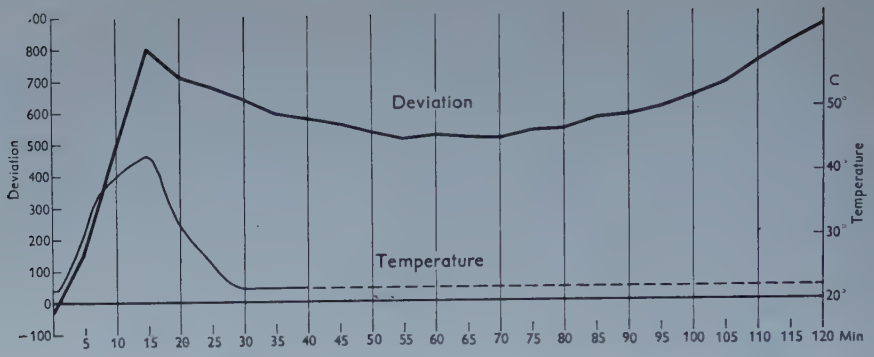

Fig. 5. The connection between temperature curve and thermotropic curvature in coleoptiles of *Avena sativa*.

tropic ones. The development of the curvature, however, varies in itself.

In fig. 2, p. 554, the curvatures at a short heating of one of the flanks of the coleoptiles by 3° C. and at a continuous heating by 3.8° C., respectively, are plotted.

On a comparison between the two curves it is found that no recurvature whatever is noticeable at continuous heating. The curve passes directly into the gradually increasing curvature towards the source of heat. Of certain interest, however, is the levelling of the curve observable between 10 and 30 min., *i.e.* just when a recurvature occurs in the curve for the short heat radiation. At the latter the coleoptile is supplied with considerably less quantities of heat than at the continuous radiation.

The pronounced positive curvature at the more considerable temperature rises might be ascribed to a direct damage to the cells of the heated side, as it is here, in some cases, a question of temperatures up to 42° or 43° C.

Fitting (1907) thus considered that he had been able to establish the collapse temperature of the coleoptiles to be exactly 43° C. at normal humidity of air (50—60 %). Nybergh (1912), however, heated *Avena* coleoptiles up to 47.5° C., without inhibition of the phototropic perception. Not even heating for 12 hrs. at this temperature changed it in relation to that normal at room temperature. Rutgers (1912) made the same observation concerning the geotropic irritability, which was not influenced either by temperatures up to 44.5° C. I myself could also ascertain that heating up to

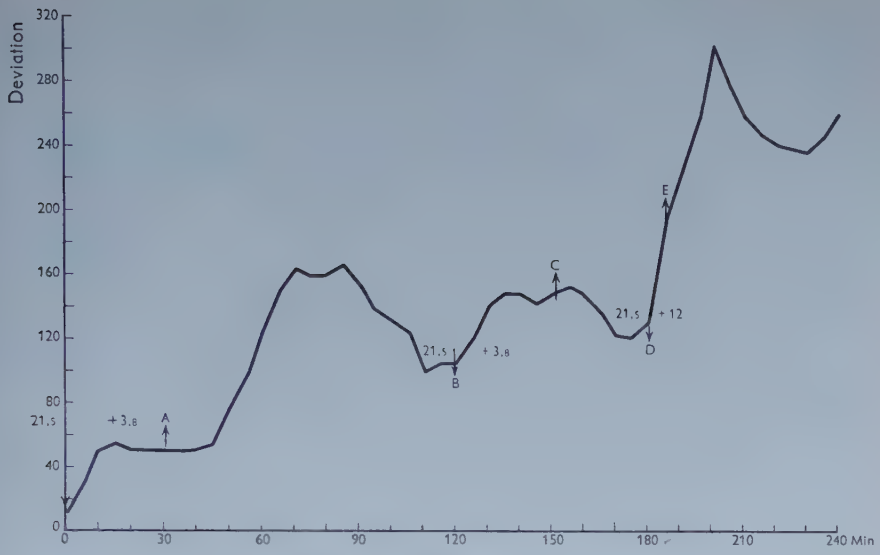

Fig. 6. Thermotropic curvatures in coleoptiles of *Avena sativa* at intermittent unilateral rises of temperature.

50° C. for 30 min. (temperature rise = 30° C.) had no influence on the responsiveness of the coleoptiles either to phototropic or geotropic irritation.

A number of curvature experiments with unilateral heat radiation of alternating long and short duration were also performed. Fig. 6 shows the curvature progress of such an experiment. The duration of the several temperature rises is here indicated by vertical arrows.

From an initial temperature of 21.5° C. the coleoptile is first exposed to heating up to a constant temperature of 25.3° C. during 30 min., a temperature rise of 3.8° C. The latter temperature is reached after 15 min. and for this time the curvature graph runs through the expected initial phase. At point A the heating is interrupted and the room temperature is restored after another 5 min. At the 40-min. point begins the third curvature phase, which leads to a — compared with the initial phase — threefold curvature value between 70 and 85 min. After that follows a recurvature — possibly caused by geotropic action.

At point B (120 mm) a renewed temperature rise to 25.3° C. occurs, which also immediately results in an increase of the curvature values similar to that of the initial phase. The increase is completed in 15 min. On the interruption of heating at point C

(150 min.), however, follows no intensified positive curvature, probably because the curvature value already attained is a threshold value in correlation to the geotropic component.

Between points D and E (180—185 min.) is finally a unilateral heating for 5 min. inserted, which results in a maximum temperature rise of 12° C. This rise provokes a new and stronger initial phase, which leads to a curvature value twice the corresponding value for the temperature rise of only 3.8° C. Similar experiments with a temperature rise of 20° C. gave still higher values.

These experiments support the hypothesis that another provoking factor than the curvature phase proper, which sets in later, must be made responsible for the very initial phase.

The nutations of the coleoptile apex in Avena.

Even Charles Darwin (1880) subjected the nutations to a close study, and Rothers (1896) states that the apex of the *Avena* coleoptile can nutate during 60 min. with an amplitude of more than 1 cm. Blaauw (1914, 1915) measured the angles of the *Helianthus* hypocotyl in rotating nutation and obtained values between 15° and 20°.

Several authors have attempted to eliminate the source of error implied by these nutation movements by using more or less ingeniously constructed, so-called auxanometers. It has been rightly remarked, however, that these instruments do not always exclude the possibility of tigmonastic irritations.

Beyer (1927) therefore tried otherwise to eliminate the disturbing nutations, viz. by allowing the seeds of the experimental material to swell in daylight. While seedlings grown entirely in darkness always showed a strong development of the mesocotyl, those grown out of seeds swelled in light showed a very low development of that organ as well as quite inconsiderable nutation movements. This inhibiting influence of light on the growth of the mesocotyl was later closely studied by Hamada (1931). He found that even a preirradiation of the seeds for 2 hrs. caused a distinct inhibition of growth in the mesocotyl, while the coleoptile growth remained constant.

Even if the development of the mesocotyl has been inhibited by the irradiation method — as has been the case in this investigation in its entirety — this does not appear wholly to exclude small nutations of the coleoptile apex, which is evident from the experiments represented in tables I—VI.

Table VII. Nutations of the coleoptile apex in the »Primus» oats (temp. in experiments I and IV: 15° C., III: 16° C., in II, V, and VI: 14° C.).

Time	5	10	15	20	25	30	35	40	45	50	55	60
Length of the coleoptile												
I. 10 mm	1	2	4	4	5	6	4	4	4	3	1	0
	1	2	4	6	6	6	7	8	9	9	8	8
II. 15 mm	0	0	2	4	4	4	6	7	7	8	5	4
	2	4	6	6	8	10	12	18	21	25	21	18
III. 17 mm	3	8	9	12	10	7	6	4	2	0	−2	−2
	2	3	10	13	15	13	8	8	6	2	2	0
IV. 22 mm	2	4	6	10	14	14	12	8	6	5	10	18
	4	8	9	10	11	15	19	20	25	30	30	26
V. 25 mm	−7	−12	−18	−23	−28	32	−36	−40	−42	−42	−37	−30
	3	5	7	8	6	1	−4	−10	−14	−20	−22	−13
VI. 28 mm	−5	−4	−1	0	5	8	10	13	19	20	20	22
	0	−3	−5	−7	1	1	2	6	13	20	25	26

Time	65	70	75	80	85	90	95	100	105	110	115	120
I.	−1	0	2	3	4	6	7	8	8	7	6	4
	7	5	4	7	10	12	11	10	8	5	3	4
II.	2	0	0	−2	−6	−8	−10	−11	−10	−8	−6	−4
	16	12	10	10	10	8	5	2	0	−2	5	−4
III.	−2	1	1	2	−1	−3	−5	−8	−12	−14	−15	−12
	−4	−3	0	4	6	6	7	8	8	8	6	4
IV.	23	26	26	20	16	11	14	20	26	32	38	36
	22	16	13	14	14	17	20	21	23	25	23	20
V.	−28	−28	−29	−31	−30	−24	−18	−9	0	6	10	12
	−10	−6	−5	−5	0	3	6	10	15	17	18	18
VI.	23	25	23	23	27	30	32	35	35	32	27	17
	23	18	8	4	2	6	12	15	20	22	21	19

Time	125	130	135	140	145	150	155	160	165	170	175	180
I.	2	1	−2	−2	−4	−5						
	2	3	4	6	8	6						
II.	0	4	4	6	8	10	10	7	2	−2	−6	−6
	−2	2	4	−2	−6	−7	−11	−12	−10	−8	−4	−2

Time	125	130	135	140	145	150	155	160	165	170	175	180
III.	–8	–5	–4	–5	–6	–9	–12	–14	–14	–10	–6	–2
	2	–2	–6	–9	–6	–8	–8	–8	–10	–10	–12	–8
IV.	33	30	26	26	30	34						
	16	12	10	7	9	12						
V.	9	3	0	–3	–4	–8	–12	–13	–15	–10	–6	0
	16	11	8	6	4	0	–6	–10	–17	–21	–16	–7
VI.	5	–8	–16	–22	–27	–27	–24	–22	–18	–13	–10	–7
	15	14	13	18	23	27	25	24	22	20	18	13

The experimental arrangement in these experiments was as follows:

On a large, detached table in the dark room two horizontal microscopes were placed at an angle of 90° to each other. At a distance of 80 cm in front of them and in longitudinal direction of the optical axis two phototropically inactive dark room lamps were constantly burning. The specimen to be studied was placed so that its image would fall within the field of vision of both microscopes. The coleoptile was at this place at least 24 hrs. before the readings began. The adjustment to a relative zero-point on the horizontally placed micrometer scales of the resp. microscopes was made 1/2 hr. before the beginning of the experiments and without the coleoptile being disturbed at all. The microscopes were adjusted for exactly the same enlargement.

When setting up the coleoptile, I allowed a small quantity of cigar-ashes to fall freely on its apex. The most part of the ashes fell of course off, but the few particles that remained, always provided a suitable standard point for the adjustment to a definite initial position for the readings. Control experiments showed that the ashes as such had no influence at all either on the growth or on the nutation curvatures.

Fifteen experiments in all were made in this series. Only 6 of them are reported here. The readings were performed at 5-min. intervals and the divergences are stated in 1/10 dividing lines (= 8 μ). The upper line in the tables gives the ordinate values, in this case the divergences on the level through the longer axis of the coleoptile cross-section. The lower line contains the abscis values for the corresponding time intervals. The experiments are plotted in table VII and fig. 7.

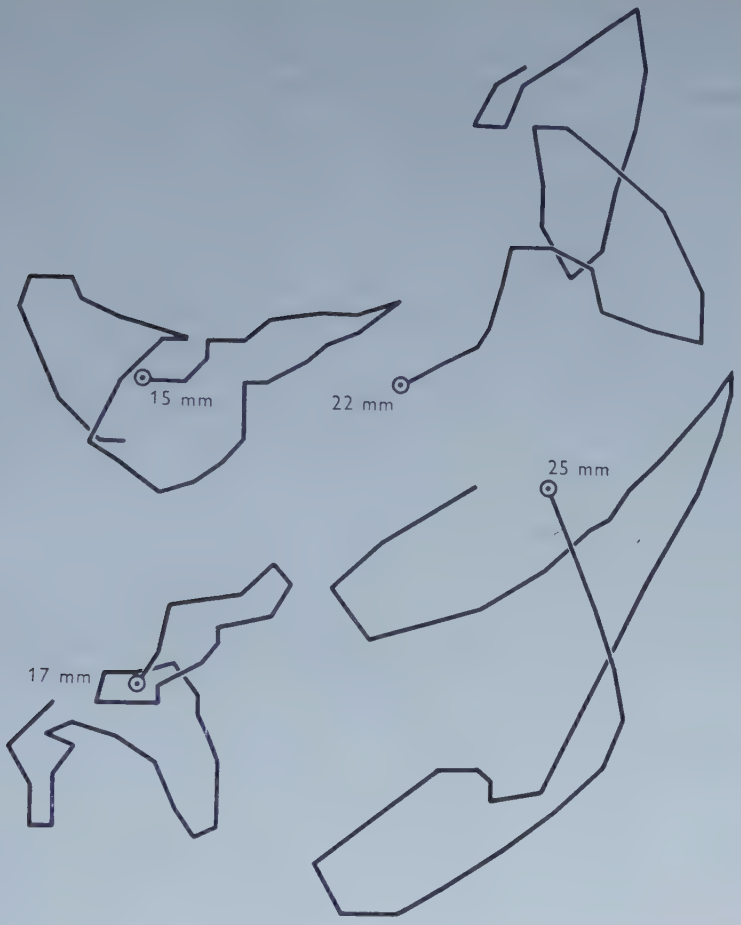

Fig. 7. Nutations of the coleoptile apex of *Avena sativa*.

Table VII and fig. 7 show that the coleoptiles perform irregular nutations, which display an amplitude increasing with the length of the coleoptile. The nutation curve often changes between twistings to the right and to the left and thus obtains the character of a torsion-equalizing nutation.

The torsion as a limiting factor by the light-orientating movements of the leaves of *Iris pseudacorus* was earlier found by the author (Erman 1926).

As is to be expected, the amplitude in one and the same coleoptile decreases in a basipetal direction, practically to disappear in the zone of its greatest elongation. This is evident from table VIII

Table VIII. Nutation movements in the zones 10 and 15 mm respectively from the apex of the coleoptile (coleoptile VI, table VII).

Col.	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90
VI	2	6	8	12	14	12	9	7	8	10	11	12	14	15	16	16	15	12
	0	−2	−2	−3	−4	−1	1	3	5	10	11	11	12	12	10	8	7	6

Col.	5	10	15	20	25	30	35	40	45	50	55	60
VI	0	0	0	−1	−1	−1	0	0	0	−2	0	0
	1	1	0	0	0	0	0	1	0	0	1	0

Fig. 8. The nutation movements in the coleoptile apex and 10 mm below the apex (dotted line).

and from the diagram for the 28 mm long coleoptile (fig. 8), where the nutation movements 10 mm and 15 mm below the coleoptile apex respectively were also registered immediately after the apical nutation.

Even the general appearance of the nutation curves and the time intervals for their turning-points made it intrinsically improb-

Table IX. Growth fluctuations and nutations of the coleoptile apex of *Avena* (»Svalövs Primus» oats). Temp. 16° C., length of the coleoptile 15 mm.

Time	5	10	15	20	25	30	35	40	45	50	55	60	min.
Growth values	3	3	4	3	3	4	3	2	2	3	3	4	
Nutation	0	2	1	1	0	0	0	−1	−2	−3	−2	−4	

Time	65	70	75	80	85	90	95	100	105	110	115	120	min.
Growth values	3	2	2	3	4	4	5	3	2	3	3	3	
Nutation	−1	−2	−2	1	1	2	2	1	2	2	1	2	

Time	125	130	135	140	145	150	155	160	165	170	175	180	min.
Growth values	3	4	2	1	3	3	1	1	1	3	4	3	
Nutation	2	1	1	0	0	−1	0	0	−2	−2	−2	−2	

Table X. Growth fluctuations and nutations of the coleoptile apex of *Avena* (»Svalövs Primus» oats). Temp. 16° C., length of the coleoptile 18 mm.

Time	5	10	15	20	25	30	35	40	45	50	55	60	min.
Growth values	3	2	3	3	3	2	3	4	1	1	3	4	
Nutation	0	1	−2	−2	−3	−3	−1	−3	−1	−1	0	0	

Time	65	70	75	80	85	90	95	100	105	110	115	120	min.
Growth values	2	2	1	3	2	2	3	4	2	2	4	3	
Nutation	1	1	2	2	2	2	3	3	3	2	−2	−1	

Time	125	130	135	140	145	150	min.
Growth values	3	3	4	3	3	2	
Nutation	−3	−2	−2	−2	−2	−3	

able that the nutations in themselves might be made responsible for the growth fluctuations (Erman 1951, p. 441).

For further control in this respect the linear micrometer of one of the microscopes was exchanged for a close-up ocular micrometer, which, by an adjustment of the tube, had been provided with the same scale value as the other microscope.

The results of two experiments from this control series are summarized in tables IX and X. The elongation is found in the second line of the tables, apical aberrations in the corresponding time intervals, in their third line.

An examination of table IX shows that the coleoptile apex for the time between 10 and 20 min. successively deviates from the perpendicular in a positive direction. These deviations, however, do not result in reduced growth values. At approximately 45 min. the coleoptile apex is back in its relative zero-position, thereupon to pass into a negative deviation. Nor does this leave its traces on the values for growth. During the period of 90—120 min. the apex returns to its zero-position (the coleoptile »pulls itself up»), without any increase in the growth values observed. Between 125 and 160 min., again, there is only a slight lateral displacement of the coleoptile apex, while the growth curve shows distinct oscillations. Similar observations can be made at an examination of table X.

Other experiments showed that no more were the nutations in file depth, *i.e.* in the direction of the optical axis, reflected in the reading curves for growth.

As a matter of fact, the nutation oscillations are rather inconsiderable in relation to the total thickness of the coleoptile. Even at the greatest deviations from the zero-point observed (about 40 dividing lines), with an absolute value of about 300 μ, this implies only a fraction of the section through the coleoptile, which amounts to about 1500 μ and more.

Perception and conduction in the thermotropic curvature.

The respective photo- and geotropic irritation is chiefly perceived by the coleoptile apex, where a quantitative accumulation of the growth factors is to be found.

Even Sierp and Seybold (1926) showed that the sensitivity to light in the extreme 2.5 millimetres of the coleoptile apex was about 1000 times as great as in the lowest zones. Lange found

that it decreases rapidly even in the uppermost half millimetre (from 7.7 at a distance of 0—50 μ to 300—400 μ). In his investigation (LANGE 1927) he obtained the following values of sensitivity to light (in mm from the apex): 0—$^1/_4$: 31832; $^1/_4$—$^1/_2$: 2116; $^1/_2$—$^3/_4$: 468; $^3/_4$—1: 99; 1—1$^1/_4$: 26; 2—2$^1/_4$: 0.017.

Even about 2 mm from the apex, the perception for light was accordingly reduced to about $^1/_{190000}$ of the corresponding one within the first $^1/_4$ of a millimetre.

SÖDING (1929) could also establish that the uppermost millimetre of the apex is the most important place for the production of growth factors, and that still 3 mm from it there is a certain small amount of them.

Are the coleoptiles decapitated, the result will be an inhibition of the lateral transport (NUERNBERGK 1933) and a considerable decrease in the phototropic curvature. If the coleoptiles are subjected to unilateral illumination immediately on the decapitation, another slight curvature is provoked; if the illumination does not take place until after 1 to 1$^1/_2$ hr., it is almost entirely absent because the free auxin has now almost completely disappeared. After another hour or so there is, however, a renewed response in the coleoptile, for the coleoptile apex has been physiologically regenerated and resumed its formation of activation of auxin (TSI TSUNG LI 1934).

On the geotropic irritation the sensitivity decresaes from the coleoptile apex downwards at a considerably lower rate than on the phototropic one. Accordingly, still 10 mm from the apex the presentation time is only about 25 times as long as in it (DOLK 1930), for the growth factors are here polarized not only in the apex. In the more basal parts a downward transport also takes place, which adds itself to the longitudinal one. This also makes the curvature spread basipetally considerably more quickly than at the phototropic one. But if, for inst., a hypocotyl of *Helianthus* is decapitated, the geotropic curvature is entirely absent, while it returns if the basal, remaining part is treated with hormone paste (RUGE 1941).

Quite different circumstances appear to exist at the thermotropic curvature. According to COLLANDER there is in that case — as mentioned above — no apical perception.

COLLANDER thus screened off the middle and lower parts of the coleoptile by means of small tinfoil contrivances, while the apex was left free. If the latter is exposed to a unilateral heat radiation, there will in most cases appear no thermotropic curvature at all.

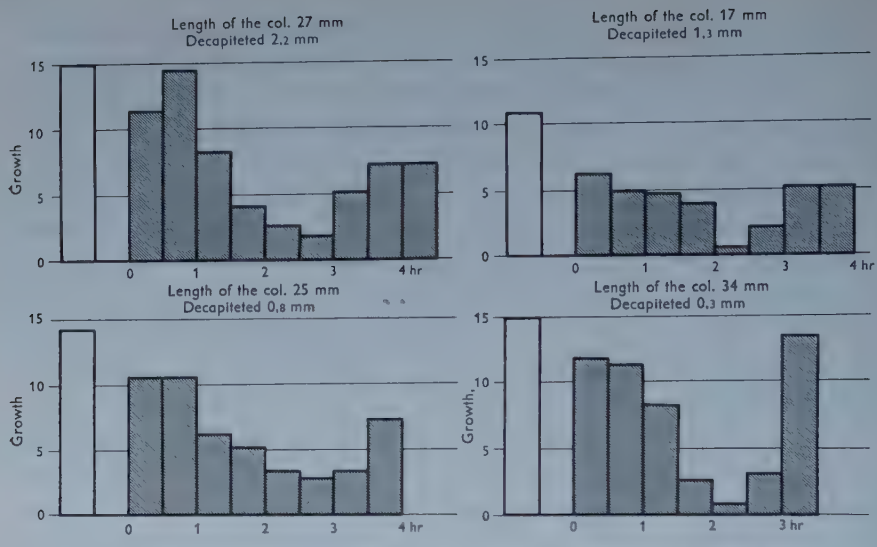

Fig. 9. The progress of regeneration in decapitated coleoptiles of *Avena* («Primus»). — The piles represent the average growth a half-hour. The detached pile corresponds to the growth for the decapitation in the same space of time.

Even this fact seems to contradict the theory of several authors that the thermo- and phototropic reactions would be closely akin. Kostytschew (1931) *int. al.* thus points out that it is, in both cases, a question of a supply of radiant energy, and that only the wave-length of the rays is different. Consequently, it would in both cases be a question of assimilation of certain amounts of energy.

If Collander's observations are correct, a thermo-curvature may consequently be provoked in decapitated coleoptiles also.

Certain difficulties always present themselves in decapitation experiments on account of the individual variation that may be shown by the coleoptiles in regard to the commencement of regeneration.

Heyn (1931) states the lapse of time between the decapitation and the noticeable regeneration to be between $1^1/_2$ and $2^1/_2$ hr. In a series of experiments I have myself sometimes, particularly with short decapitation distances, found a somewhat retarded regeneration. In fig. 9 some of these experiments are represented.

Table XI contains the values from a series of experiments with decapitated coleoptiles exposed later on to unilateral heat radiation. This was started 2 hr. after the decapitation, *i. e.* at the time when the growth rate generally proved to be at its lowest.

Table XI. Thermotropic curvatures in decapitated coleoptiles of the »Svalövs Primus» oats. ↓↑ = a temperature rise by 12° C. // = decapitation carried out 2 hrs earlier. Reading intervals, 5 min. Room temperature 14° C.

I. Length of the coleoptile 18 mm. Decapitated 6 mm.
0 0 0 –5 –5 –5 // ↓ 35 ↑ 50 45 40 40 40 35 35 40 40 40
40 40 40 40 40 40 45 45 45 45 45 45

Controlling experiment: Without rise of temp.
Length of the coleoptile 21 mm. Decapitated 8 mm.
0 –5 –5 0 5 5 // –5 –10 –01 –10 –10 –10 –5 –5 –5 –5 –5 –5
0 0 0 5 5 5 5 5 10 10 10 10

Controlling experiment: Rise of the temperature without decapitation. Thereafter decapitation and a new rise of the temp.
Length of the coleoptile 27 mm. Decapitated 6 mm.
0 5 5 10 15 20 ↓ 95 ↑ 270 280 275 250 205 150 100 60 20 10 0 //
40 180 195 210 220 230 240 245 250 255 260 265

II. Length of the coleoptile 34 mm. Decapitated 10 mm.
5 5 10 10 15 20 // ↓ 480 ↑ 560 530 535 525 540 550 565 570 570 575
580 580 585 585 585 590 590 590 590 595 595 600

Controlling experiment: Decapitation without rise of the temp.
Length of the coleoptile 30 mm. Decapitated 7 mm.
0 5 5 5 10 10 // 0 0 –10 –15 –5 –15 –15 –15 –10 –10 –10 –5 –5 0 0 0 5 5

III. Length of the coleoptile 28 mm. Decapitated 5 mm.
–5 –10 –15 –20 –25 –25 // ↓ 330 ↑ 315 320 320 320 320 320 320 320
325 325 330 330 335 340 345 350 360 365 370 375 380 285 385

IV. Length of the coleoptile 29 mm. Decapitated 3 mm.
5 5 10 10 15 15 // ↓ 525 ↑ 525 475 460 425 415 400 385 380
370 360 360 360 360 355 355 355 350 355 345 340 340 335 335 335

V. Length of the coleoptile 15 mm. Decapitated 2 mm.
0 0 5 5 5 5 // ↓ 130 ↑ 150 140 140 135 145 145 135 145
145 150 150 150 150 150 155 155 155 155 155 160 160 160 165

Figs. 10 and 11 give the development of the curvature in some decapitated and intact coleoptiles respectively of approximately the same original length and at a unilateral temperature rise of about 12° C.

The most striking in the development of the curvature is that the decapitated coleoptiles display a more forcible and more rapidly completed initial phase than the intact ones. Further, the regression phase and the eumotoric phase are not very distinct. In other words, the curvature seems to remain »fixed». This fact would

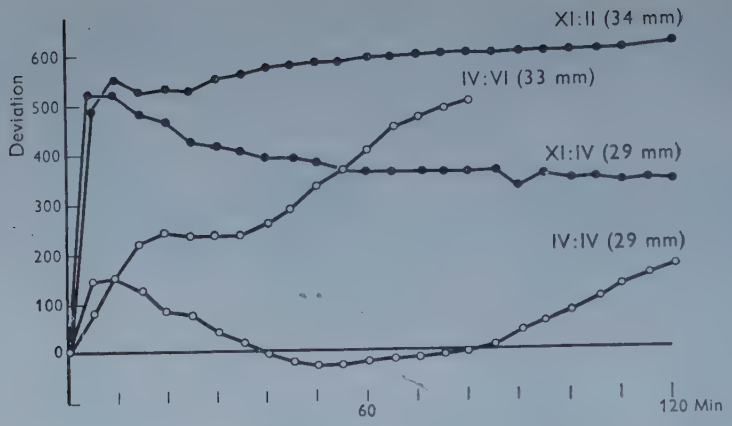

Fig. 10. The thermotropic curvature in decapitated (XI: II and XI: IV) and intact coleoptiles respectively. — »Svalövs Primus» oats.

in its turn support the supposition that a special mode of irritation would be perceived in the more apetalous parts of the coleoptile. In other words, the initial phase would be a phenomenon detached from the proper thermotropic curvature. For as shown in fig. 3 (p. 560), the definitive negative curvatures have also an initial phase of a positive character.

Collander (1919, p. 23) reconsidered the question of the thermotropic curvature possibly being due to an increase in transpiration. The increased temperature ought namely to cause an increased transpiration on the side exposed to heat. By a special experimental arrangement he excludes every possibility of such an increase but nevertheless finds a curvature directed towards the source of heat.

It is to be noticed, however, that he has never had the opportunity of observing the initial phase demonstrated here, nor has he used temperature irritations of short duration. Yet he always finds a retrogression of the attained curvature immediately after the interruption of the unilateral temperature rise. The same observation can be made in the case of the curvatures represented in fig. 3, p. 560. At the same time, however, it can be established that the successive eumotoric phase is provoked as an after-effect of the far earlier irritation, and that it seems quantitatively as well as qualitatively to be determined by the applied amount of energy. In this respect, then, it shows a distinct analogy to the phototropic curvature.

The initial phase itself, on the other hand, may very well be imagined to be provoked by the increased permeability due to the rise

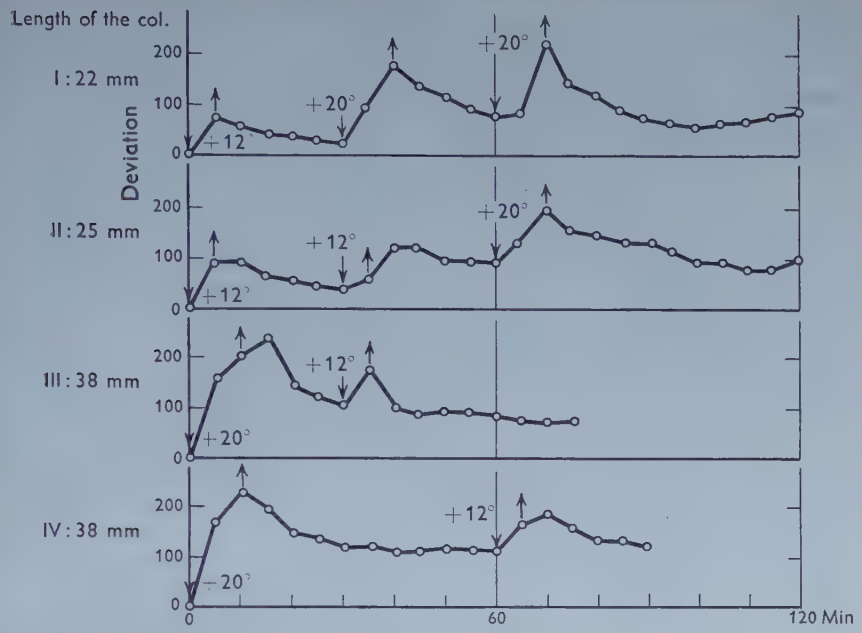

Fig. 11. Thermotropic curvatures by intermittent unilateral heating. Intact coleoptiles of *Avena sativa*.

in temperature. As the transport of the chemical growth factors, according to the investigation of Van der Weij (1934), is independent of the temperature within the interval 0°—50° C., the decrease in turgescence following as an immediate result of the increase in permeability may be chiefly responsible for the sudden initial-phase curvature, which, as mentioned above, is always positive.

The recurvature of the regression phase might then be referred to an equalization of the permeability after restoration of an all round equivalent temperature, an equalization which is more difficult in the decapitated coleoptile.

The occurrence of a special apical response is, however, also imaginable. For the investigation of this problem a series of experiments with intermittent unilateral heating were performed. The result is evident from fig. 11 and fig. 12. In this experimental series the coleoptiles in fig. 11 (I—IV) are intact, while those in fig. 12 (V—VIII) are decapitated. In all the experiments the amount of energy used corresponds to the area for definite, positive curvatures. The time of heating is evident from the distance between the arrows directed downwards and upwards respectively.

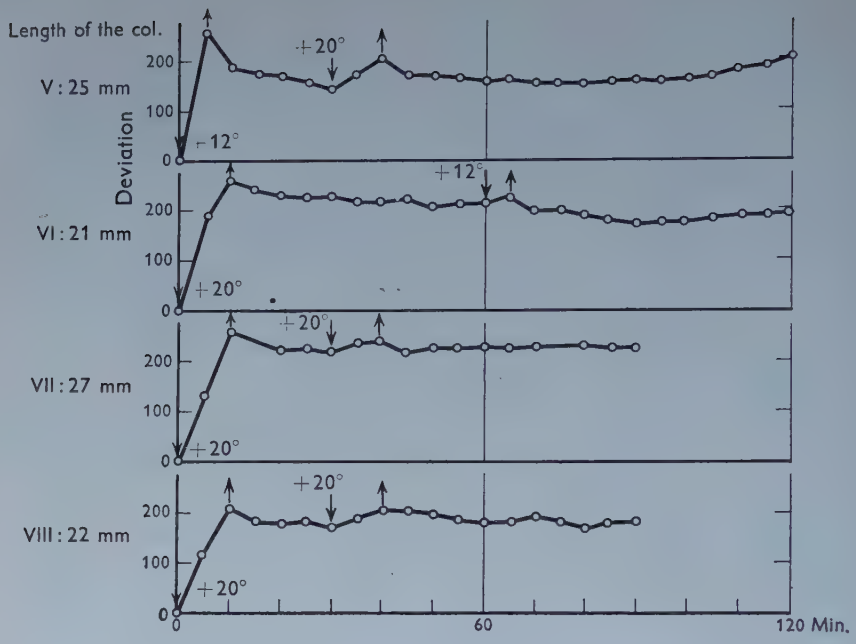

Fig. 12. Thermotropic curvatures by intermittent unilateral heating. Decapitated coleoptiles of *Avena sativa*.

As appears from a study of the curves for the four intact coleoptiles, each initial phase is here succeeded by a regression phase, which leads to a recurvature proportional in intensity to that of the preceding initial phase. At a repeated rise in temperature another distinctly marked initial phase with a successive, also distinctly marked regression phase is obtained.

Quite different does the development of the curvature appear in the four decapitated coleoptiles V—VIII (decapitated about 5 mm from the apex; experiment performed 2 hrs. after the decapitation).

An initial phase intensified in relation to the temperature rise and coleoptile length presents itself here. The succeeding regression phase is, on the other hand, considerably modified and a repeated unilateral rise in temperature produces a new, certainly, but very reduced initial-phase curvature.

Accordingly, the initial-phase curvature caused by the original unilateral heating seems to be almost irreversible in the decapitated coleoptiles.

A further support of the supposition that the very transpiration

rise is responsible for the initial-phase curvature is also provided by the frequent observation that a considerable guttation drop is squeezed out through the water fissure of the coleoptile immediately after the termination of the initial phase. At the same point of time a similar guttation drop was observed in the very section surface of the decapitated coleoptiles.

The marked decrease of the regression phase and of the subsequent initial phase on a repeated temperature rise in the decapitated coleoptiles may be dependent on the fact that a highly increased total transpiration inhibits equalizations of the permeability, or else on the exclusion of an apical reaction which in the intact coleoptiles exerts an inhibiting influence on the initial phase and consequently at the same time intensifies the regression phase.

Van Dillewijn (1927) also found — if the very coleoptile apex was kept in darkness and only the more apical parts were illuminated — three curvature phases in the phototropic curvature: a positive initial phase of short duration; a negative phase inferior to the preceding positive one; and a lasting second positive phase. He also considers that the »short response» may be traced back to an influence of changes in the permeability on the auxin transport.

Sierp (1918), Went (1925), and Filtzer (1929) have demonstrated the occurrence of two different reactions in the photo-growth phenomena, *viz.* an apical and a basal reaction. Everything speaks in favour of the thermotropic curvatures being composed of two different reactions, one of which is produced in the apex of the coleoptile, while the other one is chiefly located to its more basal parts.

The following experiment also seems to support this hypothesis.

Methods: A very thin tinfoil was wound 3 or 4 times around a wire of about the same thickness as the coleoptile. The tinfoil cylinders thus obtained in desired lengths were dipped down into vaseline (mark »Chesebrough») heated to melting. Then they were slipped on the experimental coleoptiles down to the base, whereupon these were left standing for about 24 hr. before the experiments started. The coleoptiles were then exposed to a sudden unilateral temperature rise of 12° C. (within 5 min.). The temperature rise inside the tinfoil cylinders, however, amounted to 3° C. only. The initial temperature in all the experiments was low or between 13° and 15° C.

By the arrangement described the coleoptiles were protected for

the most part of their length against an increased cuticular transpiration on heating.

By such a protection of the coleoptile against a unilaterally increased transpiration the very initial phase is, as seen from table XII and from fig. 13, wholly excluded. It is also noticeable that the coleoptile responds as if it were in its entire length within the temperature interval leading to a negative curvature.

Table XII. Thermotropic curvatures in coleoptiles of *Avena*, with a reduced opportunity of cuticular transpiration (↓↑ = rise of temperature). Room temperature 13° C. Rise of temperature 12° C.

Length of the coleoptile 38 mm. Uncovered apex 7 mm.
–5 –5 0 0 0 5 ↓ –10 ↑ –25 –45 –60 –75 –85 –90 –100 –115 –125 –140 –140
–160 –180 –200 –245 –320 –240 –260 –270 –250 –295 –300 –310
– 320 –310 –315 –320 –315 310

Length of the coleoptile 33 mm. Uncovered apex 5 mm.
5 5 10 10 10 15 ↓ 0 ↑ –15 –25 –35 –45 5–0 –55 –60 –70 –75 –80

Length of the coleoptile 28 mm. Uncovered apex 3 mm.
0 –5 –5 –5 –10 –10 ↓ –30 ↑ –60 –70 –120 –120 –125 –125 –125 –130
–135 –135 (after 2 hours = –145)

Length of the coleoptile 32 mm. Uncovered apex 10 mm.
0 0 0 –5 –5 –10 ↓ –30 ↑ –40 –50 –60 –70 –80 –90 –95 –100 –105 –110 –115

Length of the coleoptile 33 mm. Uncovered apex 10 mm.
0 –5 –10 –10 –15 15 ↓ –20 ↑ –55 –75 –115 –135 –150 –160 –170 –180
–85 –190 –95 (after 2 $^1/_2$ hours = –230)

Length of the coleoptile 26 mm. Uncovered apex 8 mm.
5 5 5 0 0 0 ↓ 0 ↑ –15 –45 –75 –80 –90 –115 –125 –130 –140 –140 –145

Length of the coleoptile 28 mm. Uncovered apex 6 mm.
0 5 5 10 10 10 ↓ –10 ↑ –50 –75 –95 –110 –125 –135 –150 –160 –170 –174 –175

Length of the coleoptile 35 mm. Uncovered apex 10 mm.
–5 –5 –10 –15 –15 –15 ↓ –10 ↑ –5 –15 –25 –35 –50 –55 –65 –70 –70 –75
–80 –90 –105 –120 –135 –145 –155 –160 –155 –155 –160 –165 –155

In the curvature graph the initial phase thus disappears and turns into a fairly evenly increasing negative curvature, which reaches its peak value within 2 $^1/_2$ hrs. after the commencement of the unilateral heating.

The initial phase of the thermotropic curve thus seems to be chiefly conditioned by the increased transpiration of the heated side.

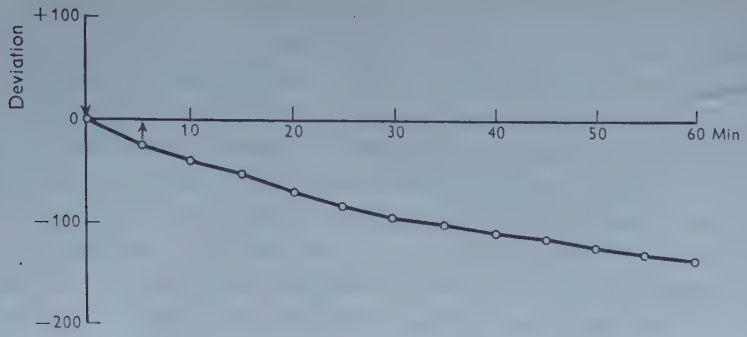

Fig. 13. The development of the thermotropic curvature in the *Avena* coleoptile at reduced cuticular transpiration. Initial temperature 13—15° C. Rise of temperature (=↓↑) 12° C. Length of the coleoptile 32 mm.

It is dependent on the length of the coleoptile as well as on the range of the rise in temperature.

The regression phase, on the other hand, seems to be conditioned by an apical response and is, probably of a purely tropistic nature.

The thermogrowth reaction and the thermotropic curvature.

While, as is evident from the preceding chapter, the initial phase of the thermotropic curvature is in all probability caused by an increase in transpiration on the heated side, the curvature cannot, however, in its continued course be explained on this basis. Every rise in temperature below optimum would then lead to a positive curvature.

Neither can the thermogrowth reaction as such (see ERMAN, 1951) be made responsible for the progress of the curvature. No doubt, the former shows a distinct growth maximum after 10 min., *i.e.* at the point of time for the maximum curvature of the initial phase, but as the height of the growth increase, as shown in table VII, 1951, is at its maximum direct proportional to the rise in temperature, and a fall in temperature from the heat side towards the side turned away from the source of heat must be assumed, the curvature ought to start with negative values. An explanation may here, as in regard to the phototropic curvature, only be gained with the support of researches on the chemical growth factors and their importance for the growth and curvature phenomena.

Specially the phototropic reactions are thoroughly investigated

in this connection, and the connection between them and the growth reactions have been discussed in detail.

Even Pisek (1926) considered that the phototropic curvature in the *Avena* coleoptile cannot be derived from the light-growth reaction but is a reaction independent of this. Sierp and Seybold (1926) showed at the same time that a decapitated coleoptile also experiences an inhibition of growth by illumination.

Beyer (1927, 1928) denies every causal connection between the light-growth reaction and the phototropic curvature. He was able to prove that decapitated *Avena* coleoptiles show growth inhibitions in light, certainly, but no curvatures. For these reasons Beyer considers that the photoblastic and phototropic reactions are two separate processes, with no mutual connection whatever.

Cholodny (1931) could confirm Beyer's observations by his experiments. Thus he found phototropic reaction capability in the coleoptiles also in cases where the light-growth reaction was absent.

A closer study of the thermogrowth reaction after decapitation has proved difficult to perform on account of the changes in form to which the section surface is afterwards subjected.

Söding (1929) studied these wound-edge changes in detail. He thinks *int. al.* (p. 205) that here it »handelt sich nur um Reizreaktionen, die durch die Verwundung als solche, nicht durch das Ausbleiben von Hormonen verursacht werden».

If such a thermogrowth reaction existed after the decapitation also, this should find expression in the mean value for the growth per 5-min. intervals during the half-hour succeeding to decapitation. This should thus always be higher than the corresponding one before the coleoptile apex is removed and the temperature rise sets in (cf. table I, 1951). This thermo-increase, however, will be covered by the general decrease in growth simultaneously caused by the decapitation, and can therefore hardly be ascertained. On that account my experiments have not been univocal either and are accordingly of no value for the discussion.

The hormonal transport at the phototropic reaction has later been the subject of a series of investigations (Bonner 1933, Went 1933 a and b, 1935, 1936, Overbeek 1933, Thimann 1934, *et al.*). Among later ones those by Asana (1938) are to be noticed, who studied the distribution of the chemical growth factors in the first negative curvature. He then found that the light-side obtained more

auxin than the shady side but could also at the same time demonstrate that the total content of auxin remained unaltered.

WILDEN (1939) investigated by means of *Avena* tests the percentage of the chemical growth factors at the first positive and negative phototropic curvature respectively as well as at the second positive one, and finds at these curvatures the following distribution: 17 %: 43 %; 62 %: 38 %, and 36 %: 64 % (the first figure refers to the luminous side).

OPPENOORTH (1939) exposed *Avena* coleoptiles to unilateral illumination. After that the coleoptile apex was cut in half and the luminous and shady side respectively was tested for the percentage of chemical growth factors. Immediately after the illumination no difference between the two sides could be observed. After 1 hr., however, the value for the shady side was more than twice the corresponding one for the luminous side. The total value was nevertheless almost unaltered. Extraction tests finally showed that the total value falls immediately after the illumination by about 30 per cent and equally for both sides. This decrease of the total value thus corresponds to the minimum of the light-growth reaction. OPPENOORTH also succeeded in showing the dependence of the light-growth reaction upon the total percentage of active chemical growth factors and that the light in itself acts inhibiting on it.

A similar unequal-sided distribution of the chemical growth factors was found by YAMANE (1940) between the shady and the luminous side in phototropically responding leaves of *Fatsia japonica*.

Thus, the cause of the phototropic curvature seems at any rate to lie in an unequal-sided distribution of auxin with the illuminated plant organ. How this unequal-sided distribution comes about, can, on the other hand, not be considered quite clear and for that reason opinions differ widely.

The different opinions may be considered to collect about three different explanations:

I. the light acts on the formation and transport of auxin within the plant;
II. the light alters the power of reaction in the cells against auxin, without any direct influence on the very transport of it;
III. the light causes the formation of an anti-auxin.

The investigators who think that the light directly influences the formation of auxin and its transport have different explanations of this.

Thus Overbeek (1933, 1936) and Oppenoorth (1939) are of opinion that the light acts inhibiting on the synthesis of auxin, while Went (1928) *et al.* believe that the transportation-power of the cells is altered by light-action. Investigations by other authors have made it clear that auxin as such is not destroyed by the visible light.

The inactivation of auxin by the influence of light is mentioned by Kögl (1937), Koningsberger and Verkaaik (1938), Gustafson (1946), Lundegårdh (1950), *et al.* Kögl thus supposes that the light-growth reaction and the phototropic curvatures are at least partly brought about by the formation of the inactive auxin-a-lactone, which however implies a sensibilisator for the visible rays. Lundegårdh also combines the photic inactivation of auxin with the formation of lumi-auxin-a-lactone.

Veldstra and Havinga (1934) found that a photoderivative, lumiautone, was formed at illumination and this is achieved by splitting off water in the photoinactivation of auxin-a-lactone.

Tang and Bonner (1947) attempt to explain the phototropic reactions by assuming an enzyme that inactivates auxin.

The supporters of the opinion of an altered power of reaction to auxin in the cells themselves are inclined to find a connection between this alteration and changes in the electric polarization conditions in the vegetable organ in question. The more important of these have already been mentioned (Erman 1951, p. 443).

Several investigators think that they have been able to prove the occurrence of growth-inhibiting substances in the plant (Münch 1932, Kornmann 1935, Hemberg 1947, 1951, Linser 1948, *et al.*).

The influence of light on the formation of these substances were studied by Galston and Hand (1949), who summarize the result of their investigation as follows (p. 92): »Light greatly decreases the growth response of plants to a given supply of exogenous auxin. Analytical data and the results of experiments with synthetic auxins indicate that illumination leads to no significant alteration in auxin levels within the cell, thus inferring that the growth inhibition imposed by light is not due to auxin photoinactivation. Rather, it would appear that light, by affecting some non-auxin system, has partially blocked the chain of reactions leading to growth, thus altering plant response to auxin.

The most remarkable difference between the phototropic and the thermotropic curvature is — as already hinted at on p. 551 — that

the latter was performed by the coleoptile in its entirety and not chiefly by its apex. The intensification demonstrable in decapitated coleoptiles in the positive initial phase and the simultaneously noticeable decline in the negatively directed regression phase indicate, however, that the very apex of the coleoptile is the perception place for a specific apical reaction antagonistic to the initial phase. This it would be, then, that partly at least finds expression in the regression phase. If that is so, the regression phase ought to disappear entirely or to grow essentially weaker when the coleoptile apex is screened off.

Table XIII below contains the mean values from a series of 10 experiments, in which the coleoptile apices up to a distance of 5—10 mm were protected by tinfoil cylinders and the coleoptiles thereafter were exposed to a unilateral temperature rise of 12° C. for 5 min. (Reading interval = 5 min.) Initial temp. 18° C.

Table XIII. The thermotropic curvatures in coleoptiles of *Avena* with the apices protected by tinfoil cylinders.

↓ 56	↑ 97	119	132	133	125	122	124	112	105	99	95	92	98	102	107	113

In fig. 14 the curvature graph is based on these values represented as a line with black cickles, while the other line represents the 12° curve in coleoptiles with their apex not screened off.

The initial phase is evidently retarded in comparison with that in the free coleoptiles. Nor is there, as in the decapitated ones, any intensification of it. The protective cylinder on the coleoptile apex covers entirely the water fissure below it and thus acts inhibiting on the transpiration.

As expected, the regression phase is evidently almost completely lacking.

While, to all appearances, the total reaction is conditioned by the amount of energy supplied, certain facts indicate that the apical reaction is again determined by the intensity used. Only detailed experiments on the development of curvatures with varied intensities and amounts of energy can answer it. Further, the observation made already by COLLANDER that the eumotoric phase of the thermotropic curvature begins simultaneously all over the coleoptile in its entire length, might indicate that transverse displacements in the distribution of active auxin play a more important role than longitudinal ones.

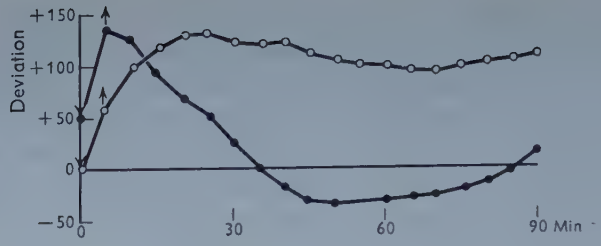

Fig. 14. The thermotropic curvatures in coleoptiles of *Avena*. (See text.)

The short presentation time of the initial phase (already after 1/2 min. a noticeable apical deviation) and the alternation of negative and positive curvature regions, finally, call attention to later investigations in the domain of viscosity research. VIRGIN (1948, 1951) accordingly emphasizes the possibility that the phototropic phenomena are connected with changes in viscosity. The statements on p. 432, ERMAN 1951 also seem to support such a theory for the thermotropic phenomena. BOTTELIER (1934) found some relationship between, respectively, a negative and a positive phototropic curvature and an increase and a decrease in the rate of protoplasmic stream after illumination. A similar correlation ought to be found even by the thermotropic curvatures.

Summary.

The thermotropic curvatures in the *Avena* coleoptile shown by COLLANDER were subjected to closer study.

On a unilateral heat radiation of short duration the coleoptiles show a curvature graph comprising the following phases (p. 560, fig. 3):

1. An immediate initial-phase of positive character. The intensity of the curvature in this is dependent on the increase in temperature and it is immediately reduced after the interruption of heating.
2. A regression phase antagonistic to the initial phase.
3. A eumotoric phase which, on considerable rises in temperature (amounts of energy) leads to a definitive, positive, thermotropic curvature towards the source of heat, but on smaller ones turns into a negative curvature away from the source of heat. The amount of energy supplied, not the intensity, seems to be responsible for the character of the eumotoric phase (p. 554, fig. 3).

Experiments with decapitated coleoptiles and coleoptiles in which the increase in transpiration was inhibited, support the theory that the initial phase of the thermotropic curvature is chiefly conditioned by the increased transpiration of the heat side (p. 580). The intensity of the initial phase is also dependent on the length of the coleoptile (p. 559).

In decapitated coleoptiles is the initial phase intensified. The successive regression phase, on the contrary, decreases. If the apical parts are protected against the unilateral heat radiation, the latter phase will be completely lacking (p. 586, fig. 14). This speaks in favour of the supposition that a reaction antagonistic to the initial phase is provoked in the more apical parts of the coleoptile.

The eumotoric phase is initiated and progresses simultaneously all over the coleoptile. It is provoked independent of the coleoptile apex. The coleoptile reacts as a whole.

Accordingly, the thermotropic curvature seems to be the resultant of separate, partly antagonistically progressing reactions.

The thermogrowth reaction as such cannot be made responsible for the thermotropic curvature development (p. 581).

The coleoptile apex is subjected to »torsion-equalizing» nutations, the amplitude of which increases with the age of the experimental material (fig. 7 and 8).

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SOME HYPOGEAL GASTEROMYCETES FROM JÄMTLAND, SWEDEN, AND ADJACENT DISTRICTS OF NORWAY.

BY

MORTEN LANGE and LILIAN E. HAWKER.

While taking part in an excursion following the Seventh International Botanical Congress, we had some opportunity to search for hypogeal fungi in Jämtland and in Norwegian localities on the border. A record of the species found is given below.

Chamonixia caespitosa Roll.

This very conspicuous fungus has previously been collected on only few occasions, so a full description of the ample material is given here.

Fruit-bodies 2—3 cm broad, 1.3—2 cm high, subglobose flattened, slightly lobed, depressed around a short stipe. Peridium separable, silky fibrillose, about 0.4 mm thick when fresh, thinner in places, white at first, slightly tinged buffish brown when spores mature, rapidly turning deep indigo blue when bruised, this colour fading to greenish blue after a while, but then kept almost unchanged in drying. Around the stipe the peridium is absent or very little developed, making the gleba visible in a meridional furrow. On mature fruit bodies the peridium often peels away in places.

Stipe about 0.4 cm high, 0.3 cm wide, solid, white, turning blue like the peridium, acuminate towards the base which continues into white rhizomorphal strands. Gleba white at first, then dark army brown through vinaceous buff, chambers small, oblong, not filled with spores at maturity. Stipe percurrent through the gleba as a narrow but distinct unbranched columella, about 0.5 mm broad.

Spores 18—20.5 × 12.7—15.2 μ, pomiform, of a rich brown colour when mature, epispore long remaining hyaline, then brown, irregularly wrinkled to form 8—10 longitudinal ribs. Apiculus short, narrow and hyaline, apex slightly papillate, though this character is often obscured by the wrinkles of the epispore. Basidia four-spored, mostly about 36 × 18 μ, in a true

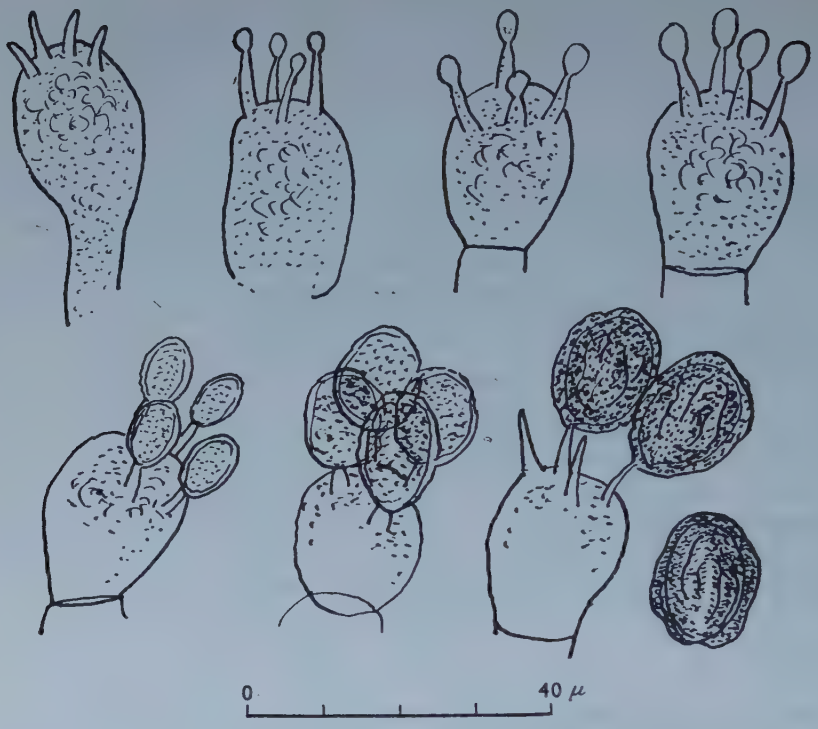

Fig. 1. *Chamonixia caespitosa*, basidia and developing spores. × 1 000.

hymenium. Trama of 4—5 μ broad hyphae, hyaline, only slightly gelatinous, without clamp connections. An indefinite subhymenium of isodiametric cells is developed.

Sections of the peridium show a thin outer layer of broad yellowish fibrils 7—9 μ broad, continuing into a layer of almost isodiametric cells somewhat radially arranged. These two layers are easily separated from an inner layer of hyphae similar to those of the trama.

The above description refers to plants in late stages of development. Very young plants which have not yet reached a diameter of more than about 2 mm have a somewhat different appearance, similar to that of young specimens of agarics. The stipe is almost as large as in fully developed specimens, and the rest of the fruit-body is convex, deeply depressed around the stipe. In section the columella is more prominent, the gleba made up of a few large chambers. The morphology of still younger stages is illustrated by Fischer (1922, 1933).

Odour and taste not distinctive.

In small clusters or solitary, hypogeous or partly exposed, in needle bed under spruce. Tevldal (Nord-Tröndelag, Meråker parish),

Fig. 2. *Chamonixia caespitosa*, two ripe spores and a younger spore (seen from apex). × 2 000.

Norway, near the Swedish border. Eight collections, July 14—26, 1950.

This peculiar fungus is probably rare. It was first described by Rolland (1899) from Chamonix in the Alps and later by Batailles (1912) also from the Alps and by Soehner (1922) who called it *Hymenogaster caerulescens*, from two localities in Bavaria, but no other records are known to us.

While the species is easily identified, much doubt prevails as to its taxonomic relations. Rolland referred it to a new genus, without discussing its taxonomic position to any great extent; while Soehner, apparently not knowing Rolland's paper, placed it in *Hymenogaster*. Cunningham (1944) and Zeller (1948) propose to include it in *Gautieria*, on account of the costate spores, typical for this genus, while Fischer (1933) considers that it is near to *Hydnangium* and *Archangeliella*, which genera include species with a similar agaricoid development and an unbranched columella. From what is known of the development of *Chamonixia* (Fischer 1922) and *Gautieria* (Fitzpatrick 1913) it is highly doubtful whether the two genera could be united, *Gautieria* being of the coralloid type, and *Chamonixia* distinctly pileate. On the other hand the spore characters of *Chamonixia* do not suggest a closer relation with *Hydnangium*. Until the classification of the Gasteromycetes is further clarified *Chamonixia* is better retained as a separate genus, probably intermediate between the pileate *Hydnangiae* and the coralloid *Gautieriae*. It would, however, be of considerable interest to get information of the development of species of *Gautieria* with a distinct peridium,

one of which, *G. Novae-Zelandiae* according to CUNNINGHAM (l. c.) is characterized by bright greenish-blue colours.

Gautieria graveolens VITT.

Several large specimens of this fungus were found at Odensala near Östersund, under pine in loose soil, rich in lime, July 22, 1950. TH. C. E. FRIES (1923) records only two localities for this species in Sweden, but we are informed that more have been added since then.

Hysterangium clathroides VITT.

A single specimen was found at Åreskutan July 23, 1950 under spruce, just under the needle bed. A larger collection was made by Professor N. F. BUCHWALD at Fårskinnsberget (Lockne parish) on the day before. According to TH. C. E. FRIES (l. c.) this plant also is only recorded twice from Sweden, one of the localities being Åreskutan.

Rhizopogon.

The delimitation of species and the settling of questions of nomenclature in this genus is a very difficult task. The material here studied includes five collections referred to two species. They are here described under the names generally employed in Scandinavian literature.

Rhizopogon roseolus (FR.) HOLLÓS.

Fruit-bodies rather small, less than 2 cm in diameter, peridium pallid, turning red in exposed parts and when touched, filaments inconspicuous and scattered. Gleba pallid whitish, the chambers rather large and remaining open.

Peridium thin in section, 130—200 μ as revived in KOH, dark reddish brown throughout, hyphae 5—6.5 μ thick. Chambers rather large and often broad, somewhat labyrinthiform, mostly 300—500 μ but up to 800 μ long, septa 70—110 μ broad, tramal hyphae 3—4 μ thick, hyaline, only slightly gelatinous, paraphyses 5—9 μ broad. Spores hyaline 7.5—10.6 × 3.3—4.5 μ averaging 9.0 × 3.7 μ mostly biguttulate, without remnants of the sterigmata, pallid olive-clay in mass.

Under *Juniperus* and *Pinus*, the soil very rich in lime. Odensala July 22, 1950. Fårskinnsberget, same date.

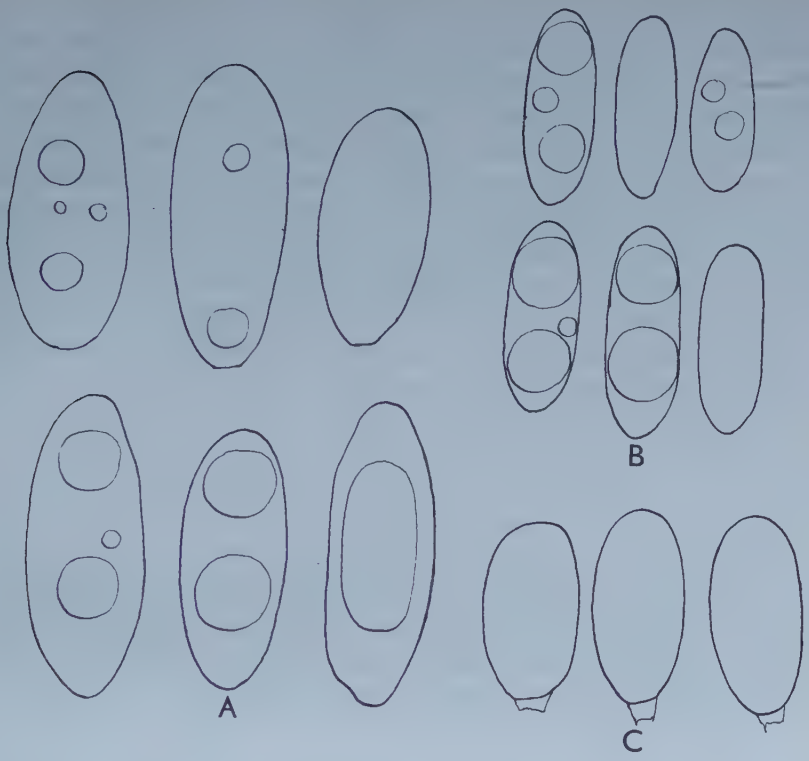

Fig. 3. Spores of *Rhizopogon*. A. *R. roseolus;* B. *R. provincialis;* C. *R. luteolus* (coll. from Denmark). All × 4 000.

Rhizopogon provincialis Tul.

Fruit-bodies rather large, about 3 cm diameter, with a few rather thick fibrils, tawny olive, paler when young, turning red when touched. Peridium thick (up to about 1 mm) reddening when cut. Gleba rather pale, dark olive buff, chambers rather large, remaining empty.

Peridium thick (200—)250—800 μ as revived in KOH, outer more narrow part dark reddish brown, inner and larger part subhyaline, hyphae 5—6 μ thick. Chambers large, often broad, somewhat labyrinthiform, mostly 300—500 μ long but seen up to 800 μ. Septa 70—110 μ broad, tramal hyphae 3—4 μ broad, the walls somewhat gelatinised. Paraphyses 4—6 μ broad.

Spores almost hyaline, olive-clay in mass, mostly biguttulate, short and narrow, 5.3—7.5 × 2.1—2.9 μ averaging 6.3 × 2.4 μ, no remnants of sterigmata seen.

Odensala, July 22, 1950, half exposed, under pines in soil rich in lime (two collections). Fårskinnsberget, same date.

The two species are easily distinguished on spore size, the characters of the peridium and the size of the paraphyses. The small-spored *R. provincialis* is further distinguished from the other small-spored species, *R. luteolus*, through more narrow spores without remnants of the sterigmata, and also through the paler colours of the spores and the reddening of the peridium. It is highly possible, that *R. provincialis* as here conceived is identical with *R. rubescens* in the sense of some authors, e.g. Zeller & Dodge (1918) and Coker & Couch (1928), *R. rubescens* and *R. roseolus* are however often regarded as synonyms. Th. C. E. Fries (l. c.) describes *R. provincialis* as rather densely clad with innate fibrils, but otherwise the description agrees with the present material.

Copenhagen and Bristol, Sept. 1951.

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DER KERNPHASENWECHSEL VON CLADOPHORA GLOMERATA.

VON

BRUNO SCHUSSNIG.

Seitdem ich im Jahre 1927 die Reduktionsteilung in den Zoosporangien von *Cladophora glomerata* festgestellt hatte, wies ich in späteren Mitteilungen darauf hin, dass sich diese Form von den anderen, auf ihren Kernphasenwechsel hin untersuchten Arten im Ablauf der Kernphasen insoferne unterscheidet, als bei ihr die mittels Zoosporen erfolgende vegetative Fortpflanzung in der Diplophase geschieht. Das bedeutet, dass vor der Ausbildung der Zoospore somatische, diploide Mitosen vor sich gehen, sodass die vegetativen Schwärmer selbst auch diploid sind. Diese Art der Fortpflanzung ist der wichtigste Vermehrungsfaktor für vorliegende Alge, während die Gametenbildung, jahreszeitlich auf das Frühjahr beschränkt, eine mehr untergeordnete Rolle spielt, zumal die Gameten selten ihre volle Reife erreichen, normale Kopulationen somit zu den Seltenheiten gehören. Sie wurden seinerzeit von Strasburger angegeben und später von H. List (1930) ein einziges Mal beobachtet.

Eine eingehendere Untersuchung, die sich auf einen Zeitraum von rund 15 Jahren erstreckt, gestattet mir nun in endgültiger, wenn auch gedrängter Form die Hauptzüge der Entwicklung von *Cladophora glomerata* zu entwerfen. Eine ausführlichere Darstellung davon mit dem vollständigen Abbildungsmaterial wird in einem anderen Zusammenhang und an anderem Orte erscheinen.

Cladophora glomerata ist eine vorwiegend diplontische Art, die sich mittels diploider Zoosporen während der ganzen Vegetationszeit (ausgenommen die Wintermonate) vermehrt. Die diploide Chromosomenzahl beträgt, zum Unterschiede von früheren eigenen und

fremden Zahlenangaben (vgl. T'SERCLAES, 1922; H. LIST, 1930; GEITLER, 1936), 96 (s. Fig. 1: 5, 8, 9). Wenn man die überwiegend vorkommende Zahl 12, die bisher bei *Cladophora*-Arten in der Haplophase festgestellt wurde, als Basis annimmt, so erscheint *Cladophora glomerata* als oktoploid. Diese Feststellung ist wichtig, weil sie gewisse Erscheinungen, die sich bei der Meiose und Gametenbildung abspielen, verständlich macht. Von den normalerweise in der Zahl 96 vorhandenen Chromosomen des Sporophyten sind 92 Autosomen und 4 selbständige, während der Interkinese längsgespalten erscheinende Heterochromosomen (nicht Chromozentren im Sinne heterochromatischer Abschnitte somatischer Chromosomen, wie dies GEITLER angibt). Von den 4 Heterochromosomen sind je zwei grösser und zwei kleiner. Eine konstante Lagebeziehung zu den in der Ein- bis Vierzahl vorhandenen Nukleolen lässt sich nicht immer nachweisen (s. Fig. 1: 1—4, 10, 11; vgl. dagegen die zu sehr schematisierten Bilder GEITLER's). Ferner muss hinzugefügt werden, dass die Chromosomenzahl nach oben schwanken kann. So konnte ich mit Bezug auf die normale Diploidzahl 96 auch triploide, mit 144 Chromosomen, oder auch davon abweichende, hyperploide Zahlen feststellen.

Die Kernteilungen, welche die Sporogenese einleiten, sind somatische Mitosen, bei denen die zwei Heterochromosomen-Paare regelmässig auf die Kerngenerationen, bis in die Zoosporenkerne, verteilt werden (s. Fig. 1: 6). Bei entsprechender Differenzierung der Präparate nimmt man in jedem Kern der fertig ausgebildeten Zoosporen je zwei grössere und zwei kleinere Heterochromosomen wahr, die in der Interphase individualisiert bleiben (Fig. 1: 7). Ebenso lassen sie sich, bei sorgfältiger Differenzierung und bei Fehlen verdeckender Strukturen, in allen Ruhekernen der vegetativen und generativen Zellen des Sporophyten feststellen (Fig. 1: 1—4).

Die Reduktionsteilung dagegen geht nur in den Gametangien, die auch morphologisch von den Zoosporangien etwas verschieden sind, vor sich. Die haploide Phase von *Cladophora glomerata* ist somit lediglich auf die reifen Gametangienkerne bzw. Gametenkerne beschränkt.

Die Gametogenese wird durch die meiotische Teilung eingeleitet. Insgesamt finden drei Teilungsschritte statt, von denen die zwei ersten zur Meiose gehören, während der dritte mitotisch, und haploid, ist. Bei ungestörtem Verlauf ist die Zahl der Gameten innerhalb eines Gametangiums mit n^3 anzusetzen. Die Kernvorgänge

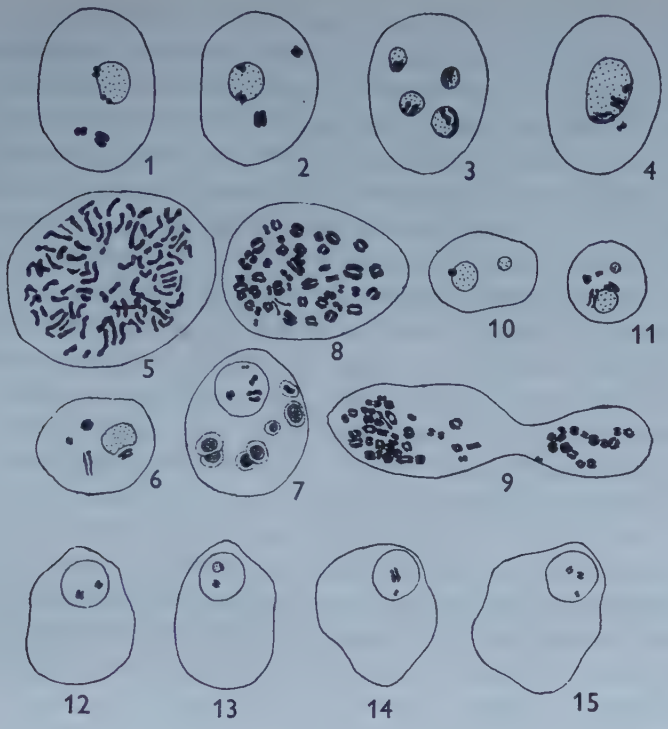

Fig. 1. *Cladophora glomerata*. 1—4 somatische Ruhekerne des Sporophyten, in denen bloss die Nukleolen (punktiert) und die Heterochromosomen eingetragen sind. 5 diploide Metaphaseplatte. 6 junger diploider Tochterkern. 7 Zoospore mit diploidem Kern mit den vier Heterochromosomen. 8 meiotische Metaphaseplatte. 9 atypische meiotische Anaphase I. 10 ein Dyadenkern. 11 ein Tetradenkern. 12—15 Gameten mit verschiedenen Heterochromosomen-Garnituren. Vergr. ca. 1250fach. (Alle Figuren sind nach den Originalzeichnungen vereinfacht wiedergegeben.)

während der Gametogenese beanspruchen ein besonderes Interesse. Die meiotischen Prozesse laufen bis zur Diakinese normal ab. In Fig. 1: 8 ist eine meiotische Metaphasenplatte dargestellt. Von da ab spielt sich der Vorgang in atypischer Form ab, d. h. eine normale Spindelbildung fällt aus, was zur Folge hat, dass die Bivalenten ungeregelt über den ganzen sich verlängernden Kernraum verstreut werden. Es liegt ein Fall von »non-disjunction» vor, was eine unregelmässige Aufteilung der homologen Paare auf die zwei, durch Einschnürung des Kernraumes gewissermassen »pseudoamitotisch» entstehenden »Kernhälften», die vielfach ungleich gross ausfallen, zur Folge hat (Fig. 1: 9). Daraus ergibt sich, dass die »Dyadenkerne» nicht nur eine ungleiche Grösse, sondern auch eine ungleiche

Anzahl von Chromosomen haben. Dies drückt sich auch in der verschiedenen Anzahl der nachweisbaren Heterochromosomen aus (Fig. 1: 10, 11). Unter den vielen sich daraus ergebenden Kombinationen sind natürlich auch solche, die »zufallsmässig» auch die richtige haploide Anzahl (48 Univalente) abbekommen.

Diese ungewöhnliche Verteilung der Chromosomen auf die beiden Dyadenkerne — und mithin auch auf die folgenden Kerngenerationen des ausreifenden Gametangiums — lässt sich zahlenmässig während der atypisch verlaufenden Anaphase I (Fig. 1: 9) wie auch während des homöotypen Teilungsschrittes feststellen. Ich erwähne hiebei, dass dieser wie auch der folgende dritte Teilungsschritt, abgesehen von der abnormen Chromosomenzahl, im Aspekt wieder normal erscheinen, obwohl mitunter auch »pseudoamitotische» Anaphasen beim II. Teilungsschritt vorkommen. Die zufallsmässige Verteilung der Chromosomen lässt sich aber auch noch daran deutlich erkennen, dass sowohl in den Interphasekernen (Fig. 1: 10, 11) als auch in den schliesslichen Gametenkernen (Fig. 1: 12—15) die Zahl der in ihnen enthaltenen Heterochromosomen schwankt, u. zw. nach den sich ergebenden Kombinationsmöglichkeiten. Die Extreme betragen 0 bzw. 4, und dazwischen findet man alle übrigen Zahlenkombinationen. Darunter auch jene, die dem Wesen der Heterochromosomen und ihrer normalen Verteilung während der Reduktionsteilung entsprechend zu erwarten ist, nämlich Gametenkerne nur mit den zwei kleineren und solche nur mit den zwei grösseren Heterochromosomen. Diese Annahme leitet sich aus den analogen Befunden bei den marinen, diplobiontischen *Cladophora*-Arten mit nur einem Heterochromosomenpaar (s. Schussnig, 1938, 1939) und unter der Annahme der polyploiden Konstitution von *Cladophora glomerata* ab. Die zufallsmässige, ungeregelte Verteilung von Auto- und Heterochromosomen auf die Gametenkerne bringt es mit sich, dass die überwiegende Zahl der Gameten noch während ihrer Entwicklung im Gametangium mehr oder weniger stark abortieren. Damit dürfte wohl auch die bereits erwähnte Tatsache von dem äusserst selten sich abspielenden Kopulationsvorgang ihre kausale Erklärung finden.

Die vegetative Vermehrung von *Cladophora glomerata* mittels diploider Zoosporen stellt zwar eine Abweichung vom Schema des antithetischen Generationswechsels bei den marinen Arten dar, sie steht aber nicht ganz isoliert da, denn ich fand bei *Cladophora utriculosa*, dass die Reduktionsteilung vor der Sporogenese ausfallen

kann, was eine Betonung der diploiden Phase, die sich hier ebenfalls mittels diploider Schwärmer (also auf homologem Wege) vermehren kann, zur Folge hat. *Cladophora glomerata* stellt somit nur den konstant gewordenen Grenzfall dieser bereits in der Gattung vorhandenen Tendenz zur Phasenverschiebung vor.

Die Verlegung der Reduktionsteilung zu Beginn der Gametogenese ist die natürliche Folge dieser Phasenverschiebung. Den atypischen Verlauf der Meiosis dagegen fasse ich als eine Folge der polyploiden Kernkonstitution auf, weil Aussenfaktoren kaum dafür in Erwägung gezogen werden können. Für die zellphysiologisch induzierte Beeinflussung des meiotischen Vorganges sprechen auch noch analoge Beobachtungen bei marinen *Cladophora*-Arten und bei *Valonia utricularis*, wo ganz ähnliche atypische Anaphasen während des ersten Teilungsschrittes zu beobachten sind, wenn sie in einem heterologen Zeitpunkt der Sporo- bzw. Gametogenese vor sich gehen (vgl. Schussnig, 1939).

Der atypische Verlauf der Meiosis und die sich daraus ergebende unregelmässige Verteilung der Chromosomen auf die Gametangien- und Gametenkerne sind wohl die Ursache für das häufige Abortieren der Gameten. Das seltene Auftreten von Kopulationen dürfte ihre Erklärung darin finden, dass eine sexuelle Verschmelzung nur dann vollzogen werden kann, wenn die Gameten Kerne mit der richtigen haploiden Chromosomenzahl (48) ausgestattet sind. Eine weitere Voraussetzung für das Gelingen einer sexuellen Reaktion dürfte ferner die sein, dass die beiden in Kopula tretenden Gameten normalerweise auch mit den richtigen Heterochromosomen ausgestattet sein müssen, d. h. der eine Partner muss in seinem Kern 46 Autosomen und die beiden grösseren Heterochromosomen, der andere 46 plus den beiden kleineren Heterochromosomen führen. Damit wäre auch ein indirekter Beweis dafür erbracht, dass die Heterochromosomen mit dem Mechanismus der Geschlechterverteilung in einem bestimmten Zusammenhang stehen.

Schliesslich geben uns die Kernvorgänge während der Gametogenese auch noch einen Hinweis darauf, wie wir uns die triploiden Individuen entstanden denken können. Da während der Anaphase I eine geregelte Aufteilung der Chromosomen unterbleibt, kann dies mitunter zur Bildung diploider Restitutionskerne führen. Es ist daher denkbar, dass ein diploider Gamet gelegentlich mit einem normal haploiden Gameten eine Verschmelzung eingeht. Jedenfalls ist dies eine — wenn auch nicht die einzige — Möglich-

keit, die uns das Auftreten triploider Pflanzen bei *Cladophora glomerata* verständlich machen kann. Auch die sonstigen abweichenden, hyperploiden Chromosomenzahlen des Sporophyten liessen sich in ähnlicher Weise erklären, wenn man annimmt, dass für das Zustandekommen eines Kopulationsaktes nicht so sehr die jeweilig vorhandene Zahl der Autosomen — wenn sie nicht allzu stark von 46 abweicht —, als vielmehr die richtige Ausstattung der Gametenkerne mit den antagonistisch wirkenden Heterochromosomen ausschlaggebend sein dürfte. Eine Entscheidung darüber können freilich nur weitere induktive Beobachtungen bringen.

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Svensk Botanisk Tidskrift. Bd 45, H. 4. 1951.

MOSSES OF NORTHWEST (DUTCH) NEW GUINEA, COLLECTED BY DR. STEN BERGMAN.

BY

EDWIN B. BARTRAM.

A limited but instructive series of mosses collected by the well-known Swedish explorer and zoologist Dr. Sten Bergman in Northwest New Guinea has been entrusted to me for study by the Naturhistoriska Riksmuseum through the kindness of Dr. Herman Persson. This collection represents 31 species distributed among 27 genera including two new species and a representative specimen of the little known *Meteoriopsis javensis* Fl.

Many years must elapse before the botanical riches of this luxuriant tropical region can be made available. Meanwhile the picture can be pieced together little by little as the vegetation of the unexplored areas becomes known. Until the actual moss flora is more clearly outlined any definite idea of its extent or affiliations can hardly be more than a subject of surmise.

A complete series of the species cited below will be deposited in the herbarium of the Naturhistoriska Riksmuseum in Stockholm and a duplicate series in the herbarium of the author.

Sphagnaceae.

Sphagnum cuspidatum Ehrh. — Slopes of the Mt. Tombrok, at the lake Anggi Gita, alt. 2000 m, No. 6.

Sphagnum Junghuhnianum D. & M. — On the way between Ransiki and the lake Anggi Gita, alt. 1250 m, No. 15. On the way between Bivac October and the lake Anggi Gita, alt. 1800 m, No. 16.

Dicranaceae.

Campylopus umbellatus (W. Arn.) Bartr. — At the lake Anggi Gita, on a vertical cliff just at the water, No. 11.

Dicranoloma Blumii (Nees) Par. — Between Bivac October and the lake Anggi Gita, alt. 1800 m, No. 32.

Dicranoloma Braunii (C. M.) Par. — Bivac October, on the ground, No. 30.

Cryptodicranum Armiti (C. M.) Bartr. — Slopes of the Mt. Tombrok, at the lake Anggi Gita, alt. 2100 m, on a tree branch, No. 4.

Leucobryaceae.

Leucobryum sanctum Hpe. — The village Waifoi on the island Waigeo, outside the westernmost peninsula of New Guinea, No. 13 in part. Sorong, on decaying stem and tree stump in the virgin forest, No. 27, 28.

Leucophanes Beccarii Broth. & Geh. — Southwest New Guinea, the island Pulau Adi, on a decaying tree stem, No. 23. Determined ex description.

Calymperaceae.

Syrrhopodon strictus Thw. & Mitt. — Slopes of the Mt. Tombrok, at the lake Anggi Gita, alt. 2100 m, No. 1. Determined ex description.

I have not been able to compare this collection with authentic material but the plants agree perfectly with the distinctions noted by Fleischer in the Laubmoosflora von Java, Vol. 1, p. 222. Previously known only from Ceylon.

Thyridium fasciculatum (Hook. & Grev.) Mitt. form. — The village Waifoi on the island Waigeo, outside the westernmost peninsula of New Guinea, No. 14.

In this collection the leaves are often bluntly pointed and provided with apical clusters of brownish septate propagula.

Calymperes hyophilaceum C. M. — Southwest New Guinea, the island Pulau Adi, on a growing tree, No. 21.

Calymperes tahitense (Sull.) Mitt. — Sorong, on a decaying tree stem in the virgin forest, No. 26.

Pottiaceae.

Trichostomum angustatum (Mitt.) Fl. — Mountain slopes on the west side of the lake Anggi Gita, alt. 2100 m, No. 9.

I have referred this collection here rather than to *T. subulifolium* Bartr. as the basal cells are lax and thin walled and the cells just above not at all porose.

Bryaceae.

Rhodobryum giganteum (Hook.) Schp. — Mountain slopes on the western side of the lake Anggi Gita, alt. 2100 m, No. 8.

Rhizogoniaceae.

Rhizogonium longiflorum (Mitt.) Jaeg. — Slopes of the Mt. Tombrok, at the lake Anggi Gita, alt. 2100 m, No. 2.

Orthotrichaceae.

Schlotheimia Bergmanii Bartr. sp. nov.

Dioica; caespitosa, caespitibus perdensis, inferne rufescentibus, superne pallide viridibus, nitidiusculis. Caulis repens, dense ramosus, ramis usque ad 2 cm altis, inferne dense ferrugineo-tomentosis. Folia ramulina imbricata, humida squarroso-patentia, apice reflexiuscula, lingulata, valde emarginata, breviter mucronata, rugulosa, 1—1.3 mm longa, ca. 0.4 mm lata; marginibus planis, integerrimus vel superne indistincte crenulatis; costa breviter excurrente; cellulis minutis, rhomboideis, incrassatis, laevibus, basilaribus linearibus, grosse papillosis. Perichaetium exsertum; folia perichaetialia ad 2.5 mm longa, emarginata, breviter mucronata; seta ca. 5 mm longa, tenuis; theca erecta, cylindrica, longicollis, sicca et deoperculata sulcata; calyptra 3 mm longa, straminea, basi lobata, apice fuscidula, vix scabra. Peristomium ignotum.

Mt. Tombrok, at the lake Anggi Gita, on a decaying stump, alt. 2250 m, No. 9.

An attractive and sharply distinctive little species characterized by the minute, emarginate leaves with the basal cells coarsely papillose or tuberculate.

Pterobryaceae.

Trachyloma indicum Mitt. — Bivac October, on growing tree 1 m above the ground, No. 31, 34.

Endotrichella latifolia Bartr. sp. nov.

Dioica; caulis secundarius simplex vel parce ramosus, ad 10 cm longus, flexuosus; folia lutescentia, nitida, sicca et humida squarroso-patentia, haud complanata, late ovato-lanceolata, sensim longe piliformiter acuminata, longitudinaliter plicata, ad 7 mm longa, 2.5 mm lata; marginibus erectis, inferne minute denticulatis, superne serrulatis; costis binis, brevis; cellulis lineari-rhomboideis, incrassatis, basilaribus longioribus, infimis fuscis. Fructus ignotus.

Bivac October, No. 38.

This species differs appreciably from *E. arfakiana* C. M. in the long, slender, almost hairlike leaf points and from *E. pilifera* BROTH. of the Philippines, in the broader leaves, squarrose-spreading on all sides and not at all complanate.

Endotrichella spinosa BARTR. — Bivac October, No. 37.

Meteoriaceae.

Aerobryopsis longissima (D. & M.) FL. var. *Dozyana* FL. — Bivac October, alt. 1500 m, No. 33.

Floribundaria floribunda (D. & M.) FL. — Bivac October, No. 43 in part.

Meteoriopsis javensis FL. — Mt. Tombrok at the lake Anggi Gita, on a decaying tree stump, No. 12.

If my interpretation is correct this is a noteworthy and highly interesting collection of a species imperfectly known only from the original gathering by JUNGHUHN in Java. Although sterile the plants are referable to *Meteoriopsis* with hardly a shadow of doubt and agree perfectly with FLEISCHER's description in the Laubmoosflora von Java, Vol. 3, pp. 841—2.

Here the plants are slender, yellowish, glossy, growing in intricate mats, secondary stems elongate, freely and irregularly branched, about 10 cm long. With the sole exception of *M. javensis* the Section *Meteoridium* is confined to the American tropics where the species are widely distributed from Mexico to Bolivia. The habit and leaf characters of *M. javensis* are quite similar to those of *M. remotifolia* (HORNSCH.) BROTH., a parallell that has been strongly stressed by CARDOT (Rev. Bryol. 38, 1911, pp. 97—99) in his remarks concerning the relationship of the Mexican moss flora with that of India.

Leskeaceae.

Thuidium plumulosum (D. & M.) BRY. JAV. — On dead wood and coral block, Southwest New Guinea, the island Pulau Adi, No. 18, 19, 20, 24, 25.

Hookeriaceae.

Chaetomitrium sp. — Bivac October, No. 40, 42.

The plants in both of these collections are sterile and epiphyllous. In the absence of fruit it is impossible to make a satisfactory determination.

Sematophyllaceae.

Trismegistia lancifolia (Harv.) Broth. var. *Korthalsii* (D. & M.) Fl. — Bivac October, on decaying tree stem, No. 29.

Brotherella falcata (D. & M.) Fl. — Bivac October, No. 36.

Acroporium hermaphroditum (C. M.) Fl.? — On the way between Bivac October and the lake Anggi Gita, alt. 1900 m, No. 17. Sterile.

Trichosteleum hamatum (D. & M.) Jaeg. — Locality lacking; probably the island Pulau Adi outside Southwest New Guinea, on the kerf of a decayed stem. The whole kerf covered with this light green moss.

Acanthorrhynchium papillatum (Harv.) Fl. — The village Waifoi on the island Waigeo outside the westernmost peninsula of New Guinea, No. 13 in part.

Hypnaceae.

Ectropothecium ichnotocladum (C. M.) Jaeg. — Mountain slopes on the western side of the lake Anggi Gita, alt. 2100 m, No. 7. Mt. Tombrok, at the lake Anggi Gita, on decaying wood, alt. 2250 m, No. 10. Bivac October, No. 39.

Dawsoniaceae.

Dawsonia gigantea C. M. — Slopes of Mt. Tombrok at the shore of the lake Anggi Gita, alt. 2100 m, No. 44. Bivac October, No. 35.

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A COMPARISON OF SOME SWEDISH AND BRITISH FORMS OF ORCHIS MACULATA L. SENS. LAT.

BY

J. HESLOP HARRISON.

Introduction.

The cytological investigations of Richardson (1935), Hagerup (1938), Heusser (1938) and Vermeulen (1938) have shown that in north western Europe *Orchis maculata* L. sens. lat. contains two chromosome series, a diploid one in which $2n = 40$, and a tetraploid with $2n = 80$. In the British Isles the two cytotypes are easily distinguishable from each other morphologically, and show in addition marked differences in their soil preferences. The diploid is a plant of meadows or open woodland on base-rich soils; the tetraploid is usually found on acid peaty soils or raw woodland humus. The presence of the two forms in the British Isles was first recognised by Webster (1886), who described an early-flowering dwarf race occurring on acid moorland in Wales as *O. maculata* var. *praecox*. Webster's description of the floral characters of this form leaves little doubt that he was dealing with a plant closely connected with that described a few years later under the name of *O. maculata* subsp. *ericetorum* by Linton (1900). To both Webster and Linton the broad-leaved plant of basic soils was the typical *O. maculata* of Linnaeus (i.e., that now known as the diploid form). Druce (1914) opposed this view, and described this plant as a new species under the name *O. fuchsii;* the Linnaean *O. maculata* to him was the plant now known as the tetraploid, Linton's subsp. *ericetorum*.

The practice of modern British authors has been to suspend judgment on the true identity of the Linnaean species, and to adopt the names *O. fuchsii* and *O. ericetorum* as sufficiently unambiguous designations for the British plants. The main differentiating features are as follows:

O. fuchsii.	*O. ericetorum.*
Chromosome number, 2n = 40.	2n = 80.
Expanded foliage leaves 3—6 in number, upper bract-like leaves, 2—6.	Foliage leaves, 2—4; bract-like leaves, 1—3.
Lowest leaf broad, obovate, rounded at the apex, flat or slightly keeled.	Lowest leaf narrow, acute, keeled, recurved.
Inflorescence conical at first, later becoming cylindrical.	Inflorescence tending to remain pyramidal.
Lateral sepals slender, erect or obliquely spreading.	Lateral sepals narrow, long, often drooping.
Labellum markedly three-lobed, the lobes sub-equal in width, the central one extending beyond the laterals; patterned with continuous double loops, lines and spots.	Labellum usually broader than long; three-lobed, the lateral lobes large, often crenulate, the central lobe small, rarely as long or longer than the laterals; patterned with irregular double loops which are often broken into short bars or dots.
Spur narrow (1—2 mm in diam.) cylindric-conical; blunt; 6—10 mm in length.	Spur filiform ($\leqq 1$ mm in diam.) hardly tapering, short (< 7 mm), sometimes very short (< 3 mm).
Robust plant of basic or mildly acid soils (pH range 5.0—8.0); woodland glades, meadows, chalk downs, occasionally on sand-dunes.	Rather more slender plant of acid peaty soils (pH range 4.0—5.5); heaths, moors, coastal pastures, woodlands.

While the morphological characters listed above serve to differentiate populations of the two cytotypes if samples of adequate size are examined, not all need be equally expressed in individual plants. Even within isolated and well delimited colonies there tends to be great variability in all of the characters which have been used as taxonomic criteria. Some of the differences between individuals can be correlated with their conditions of growth; for example, local variations in exposure and soil moisture undoubtedly affect such features as stature and leaf size. Beyond this, in populations occupying ecologically uniform habitats, there is always striking variation in flower form, colour and patterning and in leaf number and marking. Clearly the phenotypic variability reflects both genetical diversity and the plastic response of individuals to environment. It is equally apparent in the diploid and tetraploid forms,

and the concept of the species in each case must obviously be enlarged to include the observed range.

In addition to this type of local variability, a certain amount of regional differentiation is apparent in the Britannic forms of *O. maculata*. This is expressed in the same characters which show so marked local variability, and takes the form of shifts in the population mean from area to area, so that while no clear morphological discontinuities distinguish isolated colonies, they may, in the aggregate, be different from each other to a greater or lesser extent. It seems that the level at which taxonomic recognition is given to these microtopotypes[1] cannot be set in a group like this except by subjective judgment. Statistical tests may reveal »significant» differences between populations in one or more characters, but these must accumulate beyond the point of being merely biometrically detectable before they can be acknowledged in any workable system of taxonomy, although in purely evolutionary studies it may be important to recognise their presence. The case of *O. fuchsii* illustrates this point. In comparing large numbers of populations from various parts of the British Isles it has been my experience that one rarely encounters two which are inseparable statistically on some at least of the many characters in which variation occurs. All levels of differentiation appear. Small isolated colonies may show differences in such features as leaf marking which often appear purely random, and certainly not associated with any evident environmental differences. On the other hand vegetative characters may be mainly affected, and one may detect a correlation with habitat, as in the chalk-down and woodland ecodemes in southern England. At the highest level of differentiation are the regional races which have attracted sufficient attention in the field to have been graced with names — *O. fuchsii* subsp. *o'kellyi* Druce, subsp. *hebridensis* Wilm., and subsp. *cornubiensis* Pugsl. These are geographically rather well defined and in the aggregate differ from the »type» in the sense of Druce in a complex of characters, although intergrading with it in each.

Regional variation of this nature is not, of course, restricted to the British Isles -- it is a feature of *O. maculata* (and other dactylorchids) throughout north western Europe. Its »overlapping» charac-

[1] Microtopotypes -- »locally differentiated populations which may occupy similar habitats, and which are considered to have arisen by the chance fractionation of a parent population.» Gregor (1939).

ter, coupled with the intense local variation, means that descriptions based upon individuals can have little or no significance in any broad survey of the group, and there can be little doubt that a failure to appreciate this in the past has contributed to the present nomenclatural confusion. A taxonomic treatment is required which takes cognisance of the local population as the unit rather than the individual, for only thereby can the areas and affinities of the regional races be assessed. Orthodox herbarium studies involving examination of small numbers of individuals are of little value — even if herbarium material were interpretable at all in a group such as this in which pressing leads almost inevitably to the obliteration of most of the significant characters. Regional race differentiation can, however, usually be detected by the study of random samples of adequate size drawn from natural colonies in the areas under study. The biometrical analysis in such samples, preferably in the fresh state, of the characters thought best to reflect the existing geographical diversity can provide data from which the structure of the populations from which they were drawn can be estimated, and these estimates can be made the basis of more precise regional comparison. The traditional processes of plant taxonomy are not eliminated by such biometrical treatment, since as indicated above it still remains necessary to group and classify the regional races, and many of the familiar problems of promotion and subordination arise. But the method has the advantage of giving a more comprehensible and objective view of the variation in the group, and of rescuing the systematist from the labyrinth resulting from the never-ending description and naming of individual plants.

I have been interested for some years in the study of race differentiation in British dactylorchids, and the occasion of my visit to Sweden in 1950 for the 7th International Botanical Congress provided me with the opportunity of studying first hand Swedish representatives of the group. In the case of *O. maculata* sens. lat., I was able to examine several southern and central Swedish colonies in some detail and to amass a considerable amount of biometrical data, largely due to the admirably selected routes of the excursions run in conjunction with the Congress. Naturally a single season's observations are inadequate as a basis for much generalisation, but I am emboldened to publish some of my findings since correlation of work on this group in the Scandinavian and Britannic areas seems long overdue, and also because they bear upon a problem

— hardly of scientific importance, although it has long vexed British systematists — namely, which, if any, of the plants in the Britannic area should bear the name »*O. maculata* L.»

In southern Sweden the diploid and tetraploid populations of *O. maculata* sens. lat. are undoubtedly less well differentiated from each other morphologically than are the corresponding forms in the British Isles. Nevertheless, during my tour in July and August 1950, I did not encounter any which could not be referred immediately to the appropriate cytotype on the basis of labellum shape, and subsequent chromosome counts have verified the field judgment in every case. One vegetative character, namely the shape of the lowest green leaf, proved equally »good» in distinguishing diploid from tetraploid colonies. Other characters listed in the table of differentiae above as distinguishing *O. fuchsii* from *O. ericetorum* in Britain proved somewhat ineffective in discriminating the corresponding Swedish forms — notably among floral features, the shape and size of the spur, and among vegetative, the size and number of foliage leaves present at the time of flowering. Southern Swedish tetraploid *maculata* differs rather widely from British *ericetorum* in the latter characters, and I had come to consider the possibility that no Swedish populations might exist comparable with the slender-spurred, narrow-leaved British forms when I encountered a tetraploid race with these features growing in great abundance at rather high altitudes in western Jämtland in a region where the prevailing lowland form appears to be diploid.

I was thus able to examine populations of three distinct types of *O. maculata* sens. lat. in Sweden, the widespread diploid and two morphologically distinguishable tetraploid forms (referred to below as types »a» and »b»). In all about thirty colonies were examined, and of these samples of adequate size for detailed comparison were obtained from seven. Collections were made of all plants within reach in a series of random traverses across parts of the colonies selected for ecological homogeneity. In most cases the samples comprised 100 or more individuals; exigencies of time rather than the smallness of the colony prevented larger gatherings being made in the case of samples S4a and S7b.

Diploid.

S1. Omberg, Östergötland. According to Hesselman (1938) »*O. maculata* L.» is common or fairly common on Omberg. All of the

colonies encountered here in July 1950 conformed to the diploid type. The sample was drawn from a colony growing on the margin of a calcareous marsh occupying a forest glade about 1 km south of Ombergs Skidplats on the eastern slope. The soil-pH at tuber depth ranged from 7—7.5.

S2. Jormlien, Jämtland. In the neighbourhood of Jormlien *O. maculata* sens. lat. is fairly frequent. In the herb layer of the spruce forest up to an altitude of about 450 m the prevalent form is diploid. Above this level, as a component of the ground flora of the open *Betula pubescens* woods on wetter soils, the tetraploid is more common. The diploid colony sampled lay just behind Jormliens Fjällgård, at an altitude of about 350 m above sea level. The field layer of the spruce forest in this area approximates to the *Aconitum*-union described by Arnborg (1950), and the soil-pH at tuber depth was found to lie around 6.5.

Tetraploid.

S3a. Mörkö, south end of Komosse, Jönköping. The sample was taken from a very large colony south of the Mörkö—Mulseryd road about $^1/_2$ km from the former village. The ground flora of the open *Betula verrucosa* woods here is comparatively rich, and the soil-pH at tuber depth in the area occupied by the colony sampled was found to lie between 5.0 and 5.5.

S4a. Tryserum, Kalmar. The colony sampled a small and somewhat isolated one, lies to the east of the Tryserum—Valdemarsvik road in open birch wood near the village of Kägla. The soil-pH at tuber depth in the area was found to be between 4.6 and 4.8.

S5a. Vallsjö Forest, near Dorotea, Västerbotten. The sample was taken from a colony growing around the shores of the small tarn portrayed in Plate 19 of Arnborg's paper on the Vallsjö forest (1940). *O. maculata* occurs occasionally within the spruce forest itself, but the greatest concentration of individuals occurs in the mire surrounding the tarn. The pH of the ground water was found to be 4.8—5.0.

S6b. Jormlien, Jämtland. As mentioned above, the prevalent form in the neighbourhood of Jormlien up to an altitude of about 450 m is the diploid. Above this level, it is replaced by the tetraploid. The changeover is rather rapid, coinciding with the transition from the herb-rich spruce forest to the open birch forest of the higher slopes. The sample of the tetraploid population was col-

lected at a level some 200 m higher than the diploid sample S2, in a region where the soil-pH at tuber depth was *c.* 4.8.

S7b. Brattlifjället, north of Jorm, Jämtland. Here, at an altitude of about 600 m the prevalent *O. maculata* form was also found to be tetraploid. The sample was taken from a colony growing in highly exposed *Scirpus caespitosus* moor, among occasional bushes of *Betula tortuosa* and *B. nana*. The soil-pH was found to be 4.6.

For comparison with these Swedish populations, I have selected three tetraploid and three diploid populations in widely separated parts of the British Isles from which I have collected samples in other years.

The *diploid* samples all fall within the ambit of *O. fuchsii* Druce, and are as follows:

B1. Butter Wood, nr. Greywell, Hampshire. The southern English woodland-glade form of *O. fuchsii* — that taken by Druce as the type — occurs here in local abundance on mull with pH at tuber depth ranging from pH 5.0—5.8. The sample was taken in an opening in mixed oak (*Quercus robur*) wood.

B2. Nr. Ennis, Co. Clare, Ireland. Throughout this district *O. fuchsii* is plentiful in meadows on circum-neutral or slightly acid soils: the sample was taken from a colony growing in a moist meadow with soil-pH 6.5.

B3. Quarrington Hill, Co. Durham. *O. fuchsii* is one of the most abundant dactylorchids of the north east of England, and is an active colonist of many novel habitats, including quarries, clay-pits, railway embankments and the like. The colony from which this sample was drawn grows in a sheltered stretch of old-established grassland, however, on the magnesian limestone, with calcicole plants such as *Primula farinosa* — the latter an associate of the diploid form of *O. maculata* in the Omberg colonies mentioned above.

The *tetraploid* British samples are all referable to *O. ericetorum* Linton:

B4. Crane's Moor, New Forest, Hampshire. This sample was taken within the type area of *O. ericetorum*, from a colony growing in open birch woodland, a habitat similar in general aspect to that of the Jormlien colony S6b. Soil-pH 4.4—4.5.

B5. Dunlewy, Co. Donegal, Ireland. *O. ericetorum* is to be found almost everywhere on peaty soils in the west of Ireland, although

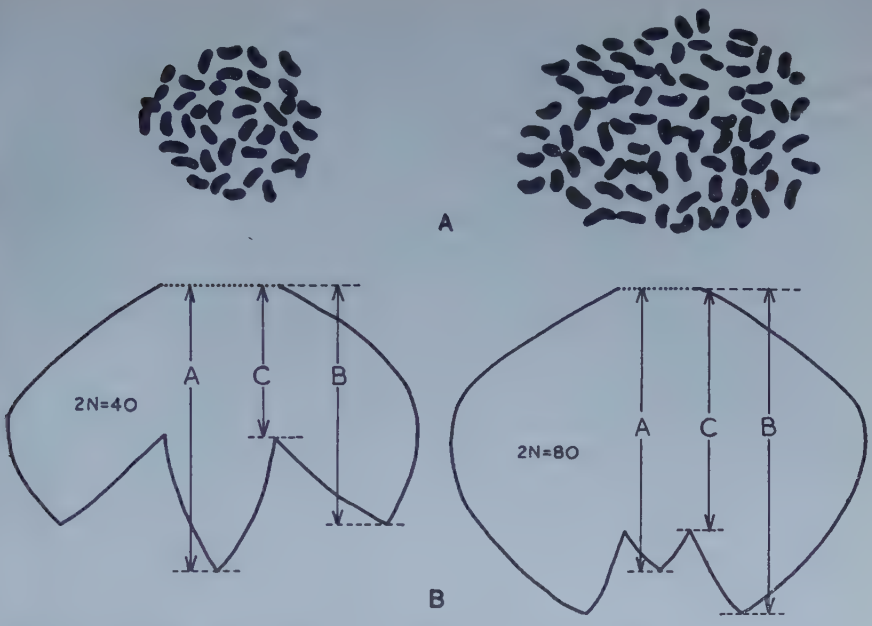


Fig. 1. A. Metaphase plates from root tips of plants from the diploid Omberg colony S1 (left, 2n = 40) and the tetraploid Komosse colony (right, 2n = 80). B. Characteristic labellum shapes found in the two cytotypes.

it is not a plant of blanket-bog proper. The sample was taken on the north eastern slopes of Errigal, at an altitude of about 350 m. Soil-pH at tuber depth, *c.* 4.5.

B6. Isle of Barra, Outer Hebrides. The sample was collected from a colony growing in highly exposed *Calluna*-moor in the west of the island, a habitat broadly comparable with that of the Swedish sample S7b. Soil-pH at tuber depth, 4.6—4.9.

Cytology.

Root-tip mitosis has been examined in material from all of the Swedish colonies discussed here, fixed in the field in Langlet's modification of Navashin's solution. A metaphase plate from a diploid plant from the Omberg population and one from a tetraploid plant from the Komosse colony S3a are illustrated in fig. 1.

The mitotic chromosomes are small and featureless, and tend to lie in groups or chains, a phenomenon more apparent in the tetraploid forms. Except in the matter of number, the karyotypes are of little systematic value, since the chromosomes of the diploid and tetraploid forms are hardly distinguishable in morphology or size.

Analysis of characters.

In the selection of characters for study from the many in which variation is apparent, attention has been directed at those floral and vegetative features which are most readily measured or assessed and which have been considered to have taxonomic value, including several of those in the above table of differentiae. The characters taken into account are: (a) labellum shape; (b) labellum length and width; (c) spur length and width; (d) plant stature; (e) leaf number; (f) length of longest and width of widest leaves; (g) leaf shape and (h) leaf marking.

Statistical data for the vegetative features were recorded as soon as possible after collecting the sample. Since critical measurements of flower parts cannot conveniently be made in the field, dissections of homotypic flowers from each plant were prepared for later attention. Mounted immediately on adhesive paper and dried under slight pressure such dissections show no significant shrinkage and retain much natural colouring indefinitely.

The statistics used in the following comparative tables are: N, the number of individuals examined; M, the arithmetic mean; σ, the standard deviation and *S.E.*, the standard error of the mean. The graphical presentation of figs. 2 and 3 perhaps needs some explanation. In each, pairs of variates are plotted, the points being inserted at the values for sample means, and distances equivalent to ± 2 (*S.E.*) are marked off each side of the mean value by bars of appropriate length. These can be used to give an approximate estimate of the significance of the difference between means where as in the majority of cases here compared the sample sizes are sensibly the same. Under these conditions, a difference between two means greater than twice the sum of their standard errors indicates $P < .005$. In the extreme cases of dissimilarity in sample sizes in the data graphed here, i.e. in the comparison of sample S7b ($N = 50$) with others in which $N \geqq 100$, using the same criterion, the value of P taken as significant never exceeds .012.

Labellum shape.

Labellum shape is probably the most consistently useful floral character in separating the two *O. maculata* cytotypes. The diagnostically important part of the variation which the labellum shows — the degree of dissection and the relative length of the lobes — can

Table I. Sample data for labellum length (A), labellum width (D) and labellum shape index $\frac{2A}{B+C}$.

Sample	N	Length in mm			Width in mm			Shape index		
		M	σ	S.E.	M	σ	S.E.	M	σ	S.E.
Diploid										
S1	117	7.70	0.87	0.08	10.75	1.56	0.14	1.33	0.11	0.010
S2	120	7.86	1.27	0.12	11.38	1.50	0.14	1.37	0.12	0.011
B1	100	7.53	0.73	0.07	10.07	1.02	0.10	1.44	0.13	0.013
B2	100	6.92	0.89	0.09	10.03	0.94	0.09	1.49	0.15	0.015
B3	100	6.99	0.77	0.08	9.85	0.97	0.10	1.43	0.12	0.012
Tetraploid										
S3a	116	8.36	1.09	0.10	10.78	1.32	0.12	1.09	0.09	0.009
S4a	54	8.31	1.16	0.16	10.39	1.14	0.16	1.07	0.08	0.011
S5a	104	8.65	0.98	0.10	11.96	1.37	0.13	1.09	0.08	0.008
S6b	100	8.17	0.89	0.09	10.65	1.13	0.11	1.12	0.09	0.009
S7b	50	7.79	0.87	0.12	9.44	1.13	0.16	1.15	0.10	0.014
B4	100	7.42	0.88	0.09	9.49	1.29	0.13	1.09	0.08	0.008
B5	100	7.10	1.10	0.11	10.77	1.57	0.16	1.06	0.07	0.007
B6	100	7.02	0.72	0.07	9.59	1.05	0.11	1.02	0.07	0.007

be estimated by means of a simple index which I have employed in analysing *O. maculata* races in Scotland (Harrison, 1948). The index is the ratio $\frac{2A}{B+C}$, the measurements having the significance shown in fig. 1, in which typical diploid and tetraploid type labella are illustrated.

Values of this index for the Swedish and British samples are given in Table I. It is evident that, so applied, this criterion gives a clear cut distinction between the diploid and tetraploid series, the means for the former all lying within the range 1.33—1.50 and of the latter between 1.01—1.15. Further, within each chromosome group there is reasonably close agreement between the Swedish and British races, and no marked difference separates the two Swedish tetraploid forms.

The visual meaning of this result is evident from Plates I, II and III. These show mounts of labella from homotypic flowers,

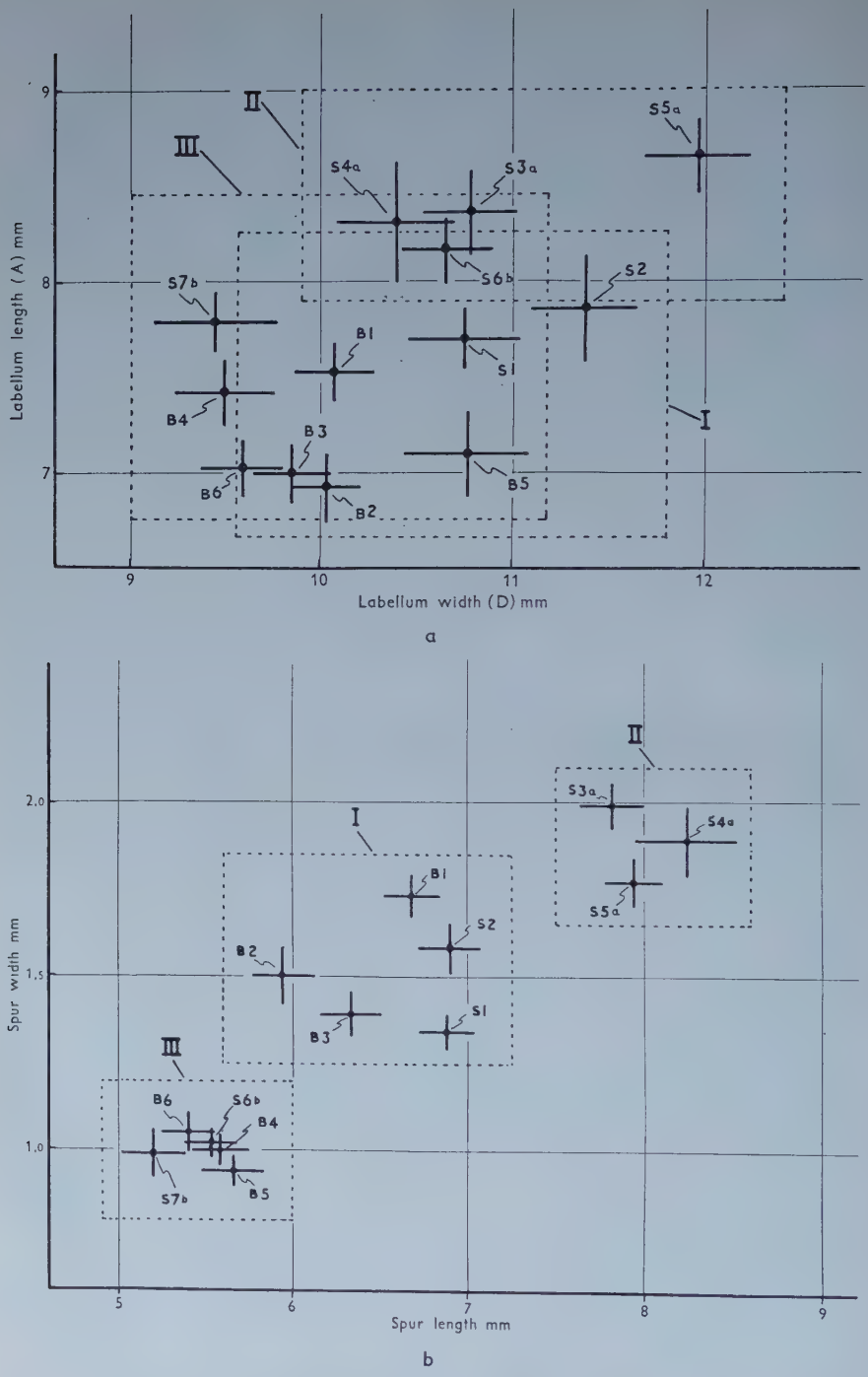
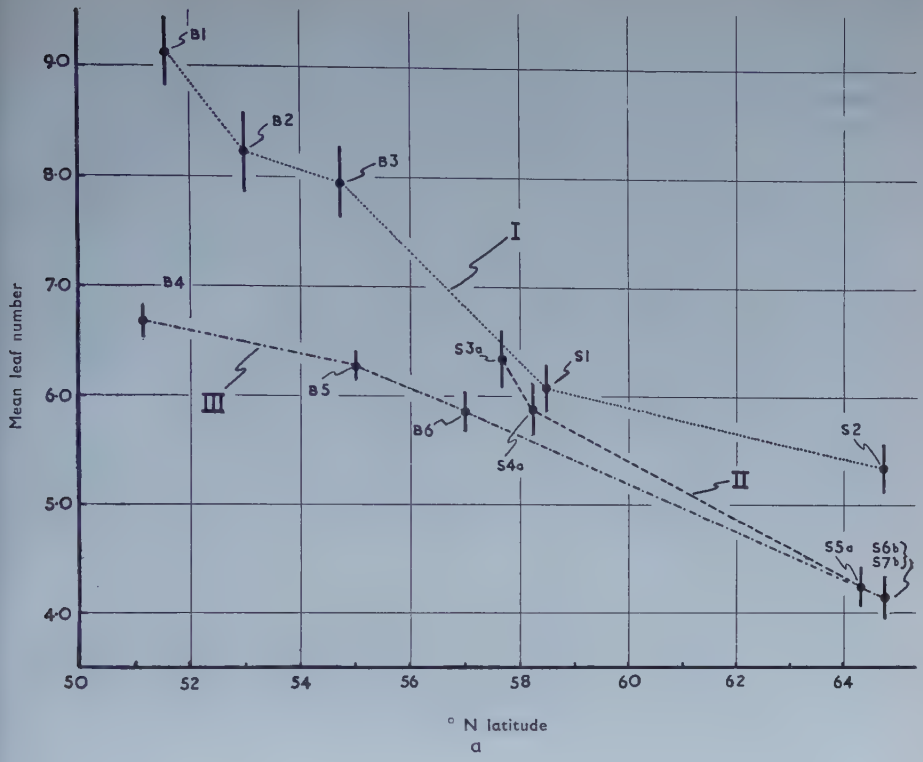


Fig. 2. a. Relation of labellum length to labellum width. b. Relation of spur length to spur width. (I diploid samples S1, S2, B1, B2; II tetraploid samples S3a, S4a, S5a; III tetraploid samples S6b, S7b, B4, B5, B6.)



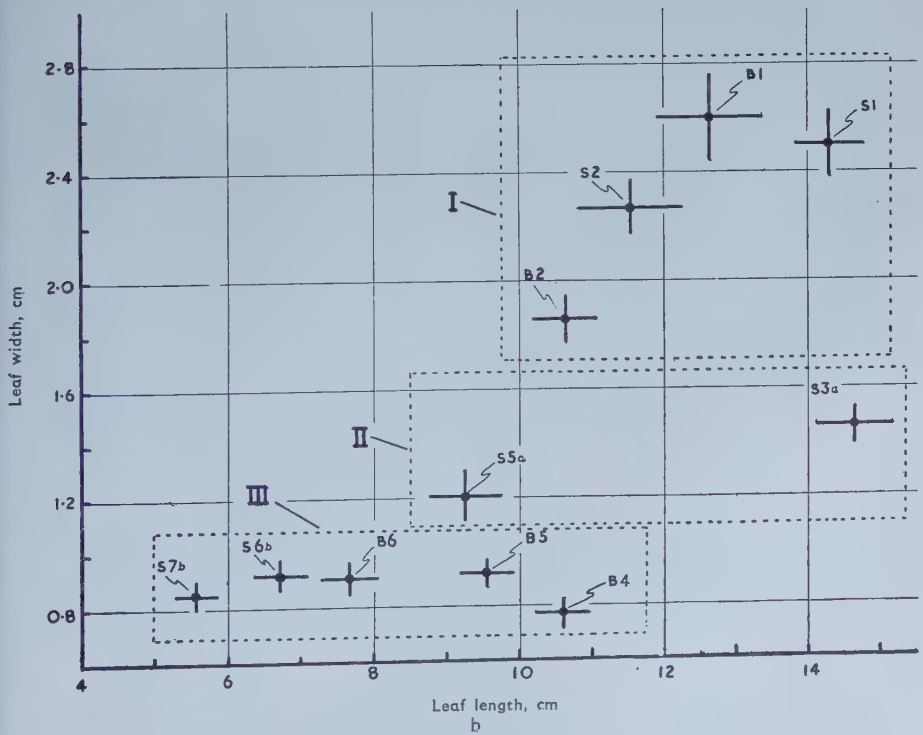
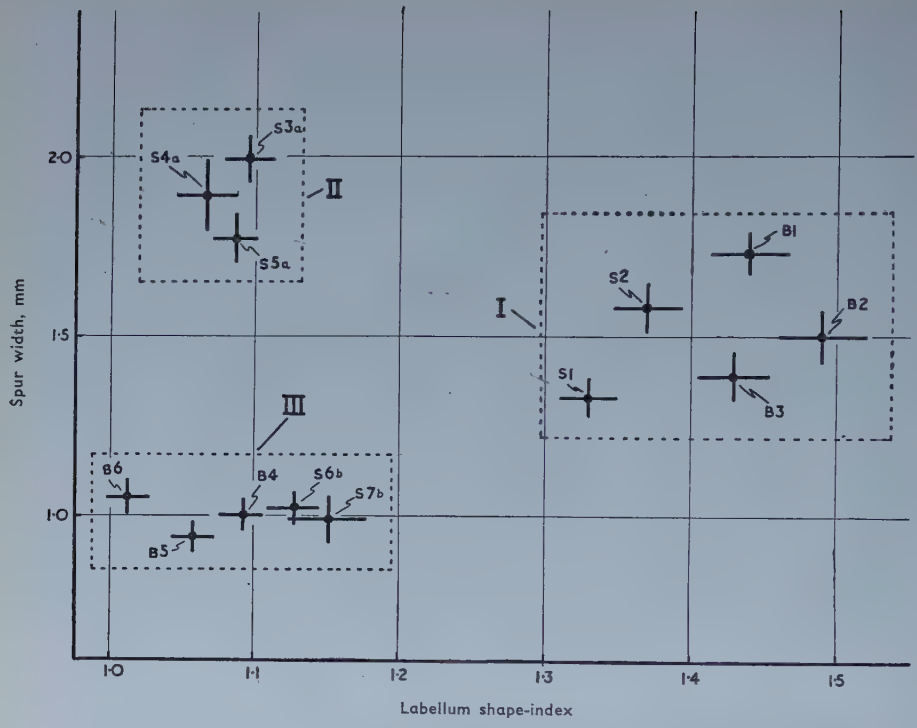
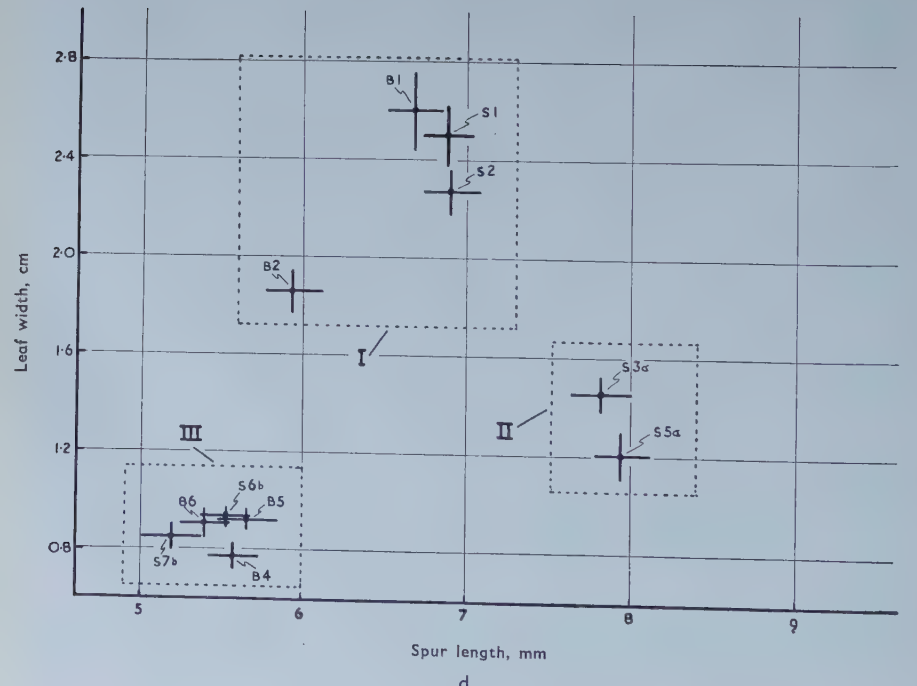


Fig. 3. a. Relation of number of leaves per plant to latitude. b. Relation of leaf length to leaf width. Groups I, II, III as in fig. 2.



c



d

Fig. 3. c. Grouping obtained taking labellum shape-index and spur width.
d. Same, using leaf width and spur length.

in each group one from each of half or more of the total numbers comprising the sample. The general similarity of labellum-form within the chromosome groups and the differences between them are clearly expressed in other features than the limited group taken into account by the index.

Labellum size.

The use of a ratio in assessing labellum shape eliminates absolute size as a variable. The sample values for the actual linear dimensions *A* and *D* are given in Table I, and it is evident that they have little diagnostic significance in that they fail to group the samples in any particular manner. Fig. 2 a shows a slight association between *A* and *D:* populations with the widest labella tend also to have the longest. There is also some suggestion that in general the labellum is rather larger in the Swedish than in the British samples in both chromosome series.

Spur size.

Sample parameters for spur length and width when flattened are given in Table II.

As indicated in the table of differentiae above, relative spur size is generally a clear discriminating feature between the two cytological series in the British Isles. This emerges from the data of Table II relevant to the Britannic area: in both spur length and width the diploid sample means are greater than the corresponding tetraploid means.

The association breaks down completely in the case of the Swedish colonies. Whereas there is reasonable agreement between the British and Swedish diploid samples, the Swedish tetraploids fall into two groups. In one of these (the series suffixed »a») the sample means for spur size considerably exceed those for the diploid series, while in the other (samples suffixed »b») they are less, and correspond closely with those of the samples of the tetraploid British *O. ericetorum*. This is most clearly brought out in fig. 2 b, where the association between spur length and spur width is shown. The samples form the following groups:

I. diploid, British and Swedish;
II. tetraploid, Swedish samples »a» only;
III. tetraploid, including Swedish samples »b» and British *O. ericetorum*.

Table II. Sample data for spur length and width.

Sample	N	Length in mm			Width in mm		
		M	σ	*S.E.*	*M*	σ	*S.E.*
Diploid							
S1	117	6.88	0.82	0.08	1.33	0.27	0.025
S2	120	6.90	0.89	0.08	1.58	0.35	0.032
B1	100	6.59	0.78	0.08	1.73	0.29	0.029
B2	100	5.95	0.94	0.09	1.50	0.36	0.036
B3	100	6.33	0.89	0.09	1.39	0.32	0.032
Tetraploid							
S3a	116	7.82	0.96	0.09	1.99	0.35	0.033
S4a	54	8.24	1.05	0.14	1.89	0.36	0.049
S5a	104	7.94	0.82	0.08	1.77	0.35	0.034
S6b	100	5.53	0.77	0.08	1.02	0.19	0.019
S7b	50	5.20	0.65	0.09	0.99	0.21	0.034
B4	100	5.58	0.87	0.09	1.00	0.22	0.022
B5	100	5.66	0.92	0.09	0.94	0.21	0.021
B6	100	5.41	0.78	0.08	1.05	0.26	0.026

The two Swedish tetraploid groups can be separated on the basis of the ratio labellum length/spur length, a feature probably more readily observed in the field than absolute size. In series »a» this ratio lies within the range 1.01—1.09 (i.e. spur and labellum are roughly equal in length) while in the two »b» samples it has the values 1.48 and 1.50 (i.e. spur is about $^2/_3$ length of the labellum).

Stature and leaf number (Table III).

The stature of each plant was measured from the part which can be removed from the ground by a vertical pull at the level of the lowest leaves. The stem breaks normally just above the tubers, and this measurement thus represents the total height of the plant less the length of the tubers. In assessing the number of leaves, the lowest green leaf is taken as the first, and that just below the inflorescence as the last even although it may be scale- or bract-like. The two or three scale leaves which invest the stem just above the tubers have been ignored in counting the number of leaves.

Table III. Sample data for stature and number of leaves per plant.

Sample	N	Stature in cm			Leaf number		
		M	σ	S.E.	M	σ	S.E.
Diploid							
S1	100	48.4	7.7	0.77	6.07	1.14	0.11
S2	100	44.2	9.9	0.99	5.34	1.05	0.11
B1	100	42.1	9.8	0.98	9.15	1.53	0.15
B2	100	38.5	8.1	0.81	8.22	1.77	0.18
B3	100	29.5	5.4	0.54	7.98	1.61	0.16
Tetraploid							
S3a	107	45.3	7.7	0.74	6.34	1.23	0.12
S4a	54	38.0	6.3	0.86	5.87	0.86	0.12
S5a	100	37.4	4.9	0.49	4.23	0.91	0.09
S6b	116	26.3	3.7	0.35	4.19	0.66	0.06
S7b	50	22.6	3.4	0.48	3.99	0.81	0.11
B4	100	23.1	5.0	0.50	6.67	1.04	0.10
B5	100	23.7	3.8	0.38	6.28	0.64	0.06
B6	100	18.9	3.6	0.36	5.87	0.94	0.09

Within populations of *O. maculata* sens. lat. growing in reasonably uniform habitats there is usually a positive correlation between plant stature at the time of flowering and number of leaves present, r usually lying between -0.4 and $+0.5$. Comparison of numerous isolated populations in Britain has, however, shown that inter-population correlation between these characters is not to be expected; it does not follow that tall-growing colonies are those with many leaves and dwarf colonies those with few. Within a population occupying a uniform habitat in which all plants receive similar amounts of illumination there is a tendency for internode development to be fairly uniform from plant to plant; variation in number of internodes (thus number of leaves) contributes at least as much to the total variability in stature as does variation in the length of the internodes themselves. It follows therefore that there will tend to be a correlation between stem length and leaf number — one which is, of course, actually observed. It seems probable, however, that internode number and internode length are not governed by closely related physiological systems. If the findings of Purvis and Gregory

Fig. 4. a. Broadest and longest leaves from six plants of *O. fuchsii* from colony B1. b. Equivalent leaves from six plants from Swedish diploid colony S1.

(1937) and others working with cereals are of general application to monocotyledons in which a determinate number of leaves is produced before the onset of flowering, the number of leaves formed is controlled by the temperature and conditions of day-length prevailing during the early developmental phases. In dactylorchids internode extension follows the differentiation of leaf primordia, and the final length attained depends on, among other factors, the intensity of light received during the period of growth. This, of course, will be affected by the density and height of the vegetation in which the plants are growing, factors which cannot influence temperature or photoperiodic régime during the earlier leaf-forming period.

The relationship of mean leaf number for the 5 diploid samples (I) and the two series of tetraploid samples (II and III) to the latitude of the colonies from which they were drawn is shown in fig. 4. The association is unequivocal; in each case there is a regular and significant increase in leaf number from north to south. The occurrence of parallel and independent clinal variation in the two cytological series leaves little doubt that this attribute, leaf number, is gov-

erned by some external factor — presumably day-length during the leaf initiation period, itself a function of latitude. A similar relationship between latitude and leaf number is evident in other dactylorchids: for example, I have encountered it in biometric comparison of Scandinavian and British populations of *O. incarnata* L. (*O. latifolia* L. sec. Pugsl.) and *O. cruenta* Müll. The phenomenon has been observed previously: as pointed out by Vermeulen (1947), it was commented upon by Klinge as long ago as 1899: »Es ist hier für die Arten in Bezug auf die Blattzahl folgendes einzuschalten, dass es hier auch auf geographischen Ort ankommt, wo das Exemplar gewachsen ist, denn je nördlicher die Art geht, um so weniger Blätter trägt sie.»

Leaf number, a feature distinguishing diploid from tetraploid colonies of *O. maculata* sens. lat. clearly enough in the British Isles, is thus of value in this respect over only limited ranges of latitude. The leaf number curves do not, however, converge at any latitude, and it is therefore fair to state that under any given set of conditions of day-length there is a tendency for the tetraploids to produce fewer leaves than the diploids.

Leaf size and shape.

Leaf size was recorded from fresh plants, the dimensions taken being length of largest leaf from opening of sheath to tip of the lamina, and maximum width of the widest leaf. In general amongst the tetraploid plants the longest leaf is also the widest. In the case of the diploids, there is a tendency for the first expanded leaf to be the widest and the second the longest. The difference is indicated in the last column of Table IV which gives the percentage of individuals in which the longest leaf was also the widest in the samples examined. The character is clearly a significant one, and is considered further below.

The data of Table IV for length of longest and width of widest leaf are graphed in fig. 3 b. The groups I, II and III (those distinguished above on floral characters) are not separable on the basis of leaf length, but are separable using leaf width as a discriminant. Again the diploid samples from the two areas fall together; in their common possession of much narrower leaves the Swedish samples »b» and British *O. ericetorum* are also associable, while Swedish samples »b» occupy an intermediate position.

Table IV. Sample data for leaf length and width.

Sample	*N*	Length in cm			Width in cm			%
		M	σ	*S.E.*	*M*	σ	*S.E.*	
Diploid								
S1	100	14.3	2.22	0.22	2.50	0.59	0.059	32
S2	50	11.5	2.62	0.37	2.32	0.38	0.051	42
B1	50	12,6	2.65	0.37	2.60	0.57	0.081	26
B2	50	10.6	1.47	0.21	1.86	0.32	0.045	—
Tetraploid								
S3a	88	14.6	2.48	0.26	1.56	0.32	0.034	82
S5a	50	9.3	1.75	0.25	1.21	0.33	0.047	74
S6b	50	6.7	1.29	0.18	0.92	0.21	0.029	78
S7b	50	5.6	1.04	0.14	0.85	0.20	0.028	66
B4	50	10.6	1.32	0.19	0.78	0.19	0.027	70
B5	50	9.5	1.33	0.19	0.92	0.19	0.027	78
B6	50	7.7	1.38	0.20	0.89	0.20	0.028	—

In last column, % individuals in which longest leaf is also the widest.

A constant difference between the tetraploid and diploid series in the Britannic area is found in the shape of the lowest leaf. In the former this is characteristically rounded and blunt or slightly »hooded», in contrast with other expanded leaves which taper to a blunt point. In the latter the lowest leaf is similar in shape to the other foliage leaves, linear or linear-lanceolate, and pointed. The differences may be grasped from the silhouettes of figs. 4 and 5, traced from flattened leaves. Fig. 4 a shows the first (broadest) and second (longest) leaves of six plants of *O. fuchsii* from the colony from which sample B1 was taken, and fig. 5 b largest (longest and widest) leaves from seven plants of the colony of *O. ericetorum* from which sample B4 was drawn. The character is equally well expressed in the corresponding Swedish groups: fig. 4 b illustrates first and second leaves from six plants from the Omberg diploid colony (sample S1) and fig. 5 c largest leaves from seven plants from the Jormlien tetraploid colony (sample S6b). Largest leaves from seven plants from the Komosse tetraploid population (sample S3a) are illustrated in fig. 5 a; although larger, these clearly conform in shape with the other tetraploids illustrated. This constant difference in leaf shape

Fig. 5. a. Largest leaves from seven plants from Swedish tetraploid colony S3a. b. Equivalent leaves from seven plants of *O. ericetorum* from colony B4. c. Equivalent leaves from seven plants from Swedish tetraploid colony S7b.

results in the fact noted above and emergent from the last column of Table IV: that, whereas in tetraploid plants the longest leaf is usually the broadest, this is the case in less than half of the diploid plants.

Leaf marking.

The incidence of leaf marking in *O. maculata* sens. lat. is strikingly variable. The distribution, size and intensity of leaf spotting differs widely from plant to plant, and colonies are often found to show distinct differences in average intensity. It is possible to make

Table V. Leaf spotting. Percentage in five grades: 1. unmarked; 2. light; 3. medium; 4. heavy; 5. very heavy.

Sample	1	2	3	4	5
Diploid					
S1	14	**42**	**31**	12	1
S2	8	**31**	**41**	20	—
B1	3	19	**39**	**37**	2
B2	7	**42**	**38**	12	1
B3	12	26	**31**	26	**5**
Tetraploid					
S3a	1	15	**30**	**38**	16
S4a	—	21	**33**	**30**	16
S5a	—	5	**31**	**44**	20
S6b	**39**	**48**	11	2	—
S7b	**60**	19	15	6	—
B4	12	**34**	**39**	15	—
B5	9	**31**	**43**	16	1
B6	16	**38**	**34**	10	2

Values in heavy face type where class contains 30 % or more.

comparisons of isolated colonies by scoring the representation in them of leaf-spot classes established arbitrarily by dividing the variation into five ranges: nil, light, medium, heavy and very heavy. The percentage representation of these classes in the samples here compared is given in Table V. The arbitrariness of this assessment invalidates its use in close biometrical comparison, but nevertheless the data of this table demonstrate one feature of the southern Swedish tetraploid colonies: the very high proportion of heavily marked plants in them and the almost complete absence of unspotted individuals. Colonies with this incidence of marking are quite exceptional in the Britannic area in either *O. fuchsii* or *O. ericetorum*, and indeed this feature is one of the most striking in these Swedish colonies to one familiar with the British plants.

Other characters.

In biometric investigations of taxonomic problems there is perhaps a tendency to overlook the wood in the anxiety to count the trees:

good discriminating features might be ignored while others less significant are given excessive attention. In the case of the dactylorchid colonies discussed here, it is perhaps worth recording that no other characters were observed during the investigation which would better serve to separate the groups, or which would place the populations examined in any other groupings. Features which contribute to the differences in appearance in the field but which are not considered above are: *Flower patterning* — the diploid populations, Swedish and British, generally show a lip pattern composed of continuous paired but usually divergent loops of reddish-purple pigment on a white or rose-pink background; the tetraploids have a similar pattern of loops, dissected more usually into short bars or dots, and less divergent (Plates I, II and III; for discussion of the basis of flower patterning see HARRISON, 1948). *Sepal posture* — in general the tetraploid plants possess drooping sepals; in the diploid they are slightly shorter, and are held more erect. *Inflorescence shape* — the pyramidal shape of the young inflorescence of *O. ericetorum* is shared also by the various Swedish tetraploid populations. *Leaf colour* — in the Swedish tetraploid populations placed together in group II, the upper surface of the leaf possesses a striking blue- or grey-green hue, a colour often found on the lower but never the upper surface of *O. fuchsii* leaves. The character is not shown by *O. ericetorum*, or by the Swedish tetraploid populations associated with it in group III.

Taxonomic conclusions and discussion.

It is evident from the above results that on the basis of relatively large differences in certain single morphological characters the populations of *O. maculata* sens. lat. can be placed in three groups. Labellum and leaf shape effectively and clearly separate the cytotypes, i.e., group I from groups II and III. These features fail to discriminate between groups II and III which can be separated, however, on the basis of leaf width and spur size. Complete discrimination of the groups can be obtained by taking the most critical of these variates in pairs. Labellum shape-index and spur width are plotted thus in fig. 3 c and leaf width and spur length in fig. 3 d. In each case the groups are clearly separated; not only are the differences between them revealed, but also the essential

unity of each is demonstrated by the consistent cohesion of the samples composing them.

The first problem in fixing the identity of these groups concerns the matter of *O. maculata* Linnaeus in sensu stricto, and may be stated succinctly — does the type description define a plant which would fall in any one of them and exclude the possibility of the others, and can the specimen in the Linnaean herbarium be placed with certainty in the same group? In *Species Plantarum* (1753) where *Orchis maculata* is first named as such by Linnaeus, the brief description given includes the following: »Nectarii labium trifidum, planum: lobis lateralibus majoribus crenatis; intermedio angustissimo, integerrimo.» There can be no reasonable doubt that this description of the labellum rules out the characteristic diploid form, but covers quite adequately that found in the tetraploids, i.e., in the plants placed in groups II and III. Nothing in the description serves to discriminate between these groups, nor is there to be found any decisive statement in the other Linnaean descriptions to which reference is made in the account in *Species Plantarum*, namely those of the *Flora Svecica* and *Iter Oeland.* of 1745, the former a restatement of a description given in *Acta Soc. Upsal.*, 1744.

The description given in *Species Plantarum* is numbered »12», and a sheet in the Linnaean herbarium labelled »*maculata*» in Linnaeus's hand-writing and carrying this number bears a single and unfortunately incomplete specimen which must presumably be taken as the type. I have examined this plant in detail, particularly with regard to the characters stressed above. The lowest leaf is missing, and therefore its shape cannot be taken into account; of the remaining six leaves, two ensheath the stem completely at the base and four are bract-like. The largest leaf remaining is lanceolate, 8.2 cm long and 0.9 cm in width. Three labella are clearly enough exposed for their shape to be observable, and there can be no doubt that they conform rather with the characteristic tetraploid form than with the diploid. The actual dimensions of the most accessible labellum of the Linnaean plant, so far as they can be determined without disturbing the mount are: labellum length (*A*) 7.75 mm; length of lateral lobes (*B*) 6.5 mm; maximum width (*D*) 7.25 mm. The value for labellum shape index is 1.12. The dimensions of the most accessible spur are: length from junction with labellum to tip, 6.6 mm; width at broadest point visible, 1.35 mm. Dactylorchid floral parts shrink much on drying, and

it is not easy to decide what allowance has to be made for this in a plant of the age of the Linnaean specimen. Since a shrinkage of more than 20 % in linear dimensions is commonly found using normal drying methods, an allowance of 10 % seems a very conservative estimate. Assuming this, the spur of the flower examined must have exceeded 7.25 mm in length and 1.48 mm in width in the living state. Using the values for sample S6b, the larger spurred of the two Swedish samples in this group, as estimates of population parameters, the chances of the Linnaean plant having been drawn from a similar population are greater than 35 : 1 against, in the case of both spur length and width. On the other hand, on the basis of these characters, the odds against this plant having come from a population with parameters similar to those here placed in group II, i.e. samples S3a, S4a and S5a, never exceed 7 : 1.

It seems therefore a fair conclusion, on the basis of the description of the *Species Plantarum* and the evidence of the plant in the Linnaean herbarium, that the original *Orchis maculata* of Linnaeus was a plant conforming with those here placed in group II, i.e., the tetraploid form most widespread and abundant on rather acid soils in southern and central Sweden.

There remains the fixation of appropriate names for the plants associated by the above analyses in groups I and III, a matter which is closely connected with the question of what rank is to be ascribed to them. The two cytotypes, as we have seen, are well distinguished from each other morphologically, have dissimilar ecological preferences, and moreover do not freely form hybrids in nature. The case for making the cytological division a primary one, and separating the diploid and tetraploid form-groups as two species is therefore unassailable. If this is done, the name *O. maculata* L. must be retained to cover the tetraploid series. The earliest description of a form from north western Europe which can now be identified as referring almost certainly to the diploid series is that given by de Brébisson in his Flora of Normandy (Ed. 1, 1836) for *O. maculata* var. *trilobata*. It seems equally certain that the var. *meyeri* of the younger Reichenbach (1851) and var. *obscura* Neuman (1909) are also based upon diploid plants. However, the first species name given to a diploid plant is that of Druce (1914), namely *O. fuchsii*, and since in accordance with Art. 58 of the International Rules of Botanical Nomenclature this constitutes

»the earliest name or epithet given to the group in its new rank», it is the valid name.

The application of the name *O. fuchsii* to the diploid forms associated in group I is thus justifiable. The British colonies from which data have been used in this account fall within the ambit of that accepted as the typical form of the species, which according to the recommendations of the International Botanical Congress of 1950 becomes *O. fuchsii* subsp. *fuchsii*. In most characters the Swedish colonies fall within the same range of variation, but may be considered to diverge to a certain extent, possibly in their larger labella, and certainly in their possession of fewer leaves. The difference in labellum size between the Swedish sample S1 and the British B1 is, however, hardly greater than that between the two Swedish samples, or between the British samples B1 and B2, and certainly does not signify a break in the variation range. The undoubtedly significant differences in leaf number can hardly be taken into account taxonomically if, as the data of fig. 3 a suggest, there is a continuous geographical gradient in this character. The conclusion is therefore that the segregation of Swedish *O. fuchsii* as a subspecies is premature on the basis of the evidence here presented.

Turning to the remaining assemblage, group III, we find that the British and Swedish samples brought together in it are in close agreement in most features, again with the exception of leaf number. Although also tetraploid, the plants falling in this group are morphologically separable from those composing group II, that is, from *O. maculata* subsp. *maculata*. The distinctions between these tetraploid races, although evident enough to be recognised in the field, certainly cannot be maintained as having specific value. The nomenclatural requirement seems to be met most adequately by a reversion to Linton's *O. maculata* subsp. *ericetorum* (1900) to cover the plants placed together here in group III, and others of the same affinity.

While the above discussion involves one of the central questions, namely the identity of *O. maculata* L. in sensu stricto, I have intentionally avoided mention here of the many other nomenclatural problems which surround the *maculata* form-complex, particularly those concerning races outside the Scandinavian and British areas. Academic argument cannot solve the problems of variation involved, which must, after all, be understood before nomenclature can be stabilised. It is unlikely that further progress can be made in understanding dactylorchid polymorphism without constant refer-

ence to plants in the field, as populations and not as abstracted individuals. Second hand views and opinions based upon two or three dried and half-decomposed individuals can help little, and such treatments as that of von Sóo (1930—40) illustrate how impotent is the collection of names and descriptions.

Among recent works in which an attempt is made to place the definition of dactylorchid taxa on a broader and biologically sounder basis is that of Vermeulen (1947). The taxonomic conclusions presented here relating to *O. maculata* L., *O. maculata* subsp. *ericetorum* Linton and *O. fuchsii* Druce are in broad agreement with his findings, although I have preferred for the moment to defer acceptance of his new genus, *Dactylorchis*. A comment is perhaps due in relation to *O. elodes* Grisebach, a plant considered to be a tetraploid and treated by Vermeulen as a subspecies of *O. maculata*. Many British authors (notably Godfery, 1921) have identified *O. ericetorum* Linton with *O. elodes* Grisebach, and there is certainly nothing in Grisebach's full description which would rule out this possibility. I nevertheless prefer not to accept it without knowledge of the tetraploid race occurring in Grisebach's type locality, Bourtranger Moor in northern Holland.

As a final comment it may be added that there are undoubtedly other Scandinavian races of the *maculata*-complex beyond those described above. In the neighbourhood of Abisko I collected plants with remarkably small numbers of leaves, with the labellum reminiscent of the type commonly found in the diploid series, but with an extraordinarily broad centre lobe. The chromosome number of these proved to be $2n = 40$. Similar plants were kindly sent to me by Mr R. Becking from northern Finland. If these plants do not constitute the »*O. maculata* var. *psychophila*» of Schlechter (1928) they are certainly closely related, and it is my regret that I was unable to obtain enough material to define this form biometrically in relation to the other Scandinavian ones I encountered.

Acknowledgements.

The collection of material in Sweden was made possible by the receipt of a grant from the Queen's University, Belfast, to which institution I wish to tender my thanks.

I have to acknowledge much assistance in the collection of material and in recording data to many members of the extremely

successful Excursion CIIId, run in conjunction with the 7th International Botanical Congress, and so ably led by Dr T. Arnborg.

I wish also to thank my wife, Dr Y. Heslop Harrison, whose continuous assistance in the biometrical work has been invaluable, and Mr R. Brinsden, A.R.P.S., who took the photographs of flower parts.

Summary.

1. Two cytotypes of *O. maculata* L. sens. lat. occur in Sweden, a diploid in which $2n = 40$ and a tetraploid in which $2n = 80$.

2. Biometrical comparison based upon large samples shows:

a. The diploid form occurring on base-rich soils in southern and central Sweden falls within the variation range of *O. fuchsii* Druce, a common dactylorchid of similar soils in Britain.

b. The widespread tetraploid form found in the same area on more acid soils has no counterpart in the British Isles, and is to be interpreted as being *O. maculata* L. sensu stricto.

c. A tetraploid race agreeing in most characters with the common tetraploid form in the British Isles is to be found at high altitudes in western Jämtland, and must be included within the ambit of *O. maculata* subsp. *ericetorum* Linton.

Explanation of the Plates.

Plate I.

Labellum mounts from homologous flowers. — A. 72 plants of *Orchis fuchsii* from colony B2, Ennis, Co. Clare, Ireland. — B. 56 plants from the Swedish diploid colony S1, Omberg, Östergötland.

Plate II.

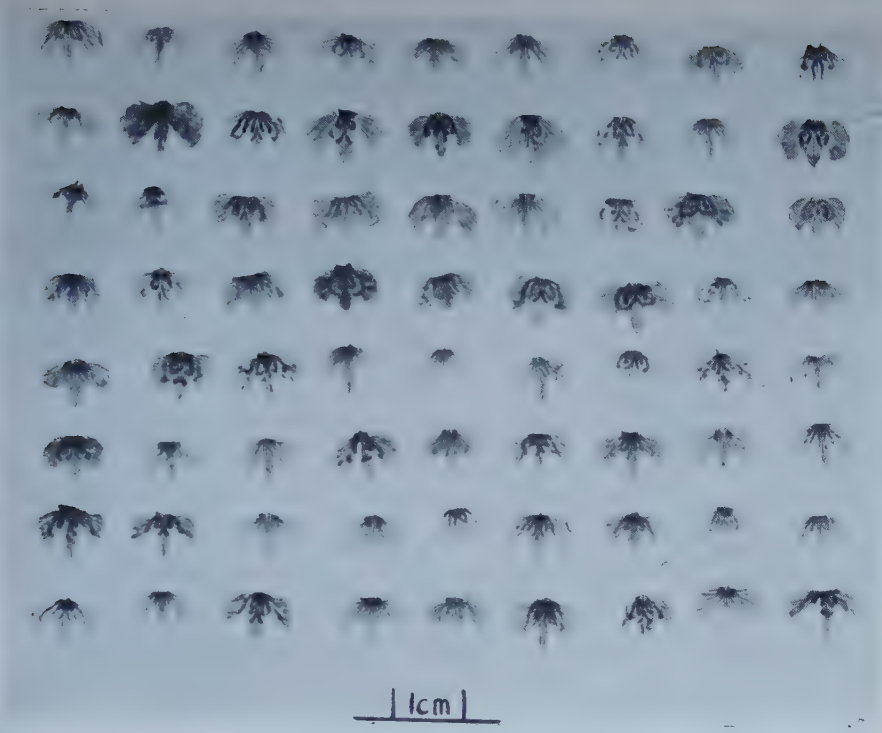
Labellum mounts from homologous flowers. — A. 52 plants from the Swedish diploid colony S2, Jormlien, Jämtland. — B. 56 plants of *O. ericetorum* from colony B5, Dunlewy, Co. Donegal, Ireland.

Plate III.

Labellum mounts from homologous flowers. — A. 63 plants from the Swedish tetraploid colony S6b, Jormlien, Jämtland. — B. 56 plants from the Swedish tetraploid colony S3a, Mörkö, Jönköping.

Plate IV.

A. Labellum mounts from homologous flowers from 48 plants from the Swedish tetraploid colony S5a, Vallsjö, Västerbotten. — B. Mounts of complete flowers from 35 plants from the Swedish tetraploid colony S3a to show spur proportions.



A

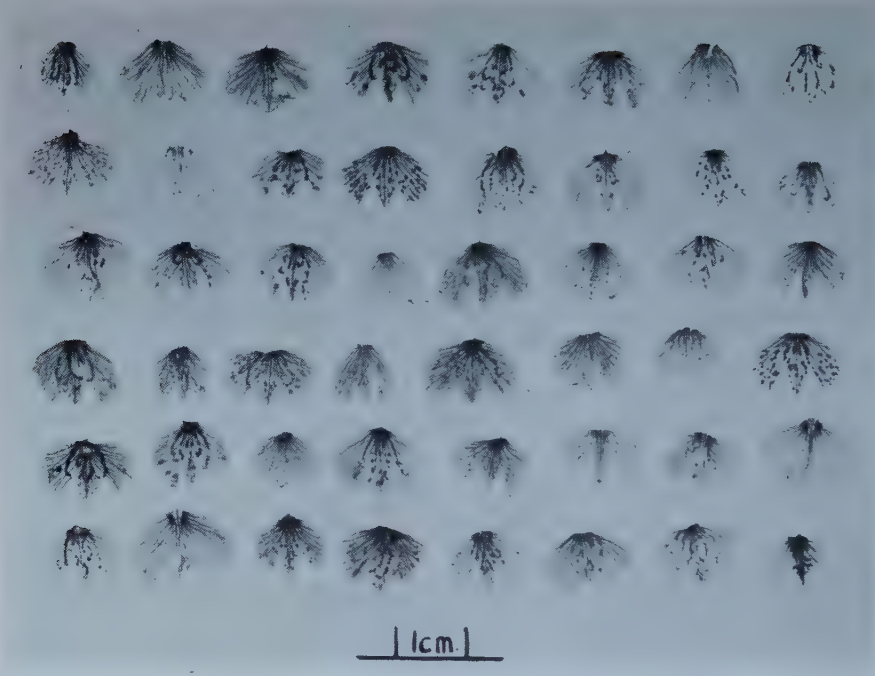
B

A

B

A

B



A

B

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ELEKTRONENMIKROSKOPISCHE UNTERSUCHUNGEN VON DIATOMEENMEMBRANEN, II.[1]

VON

R. W. KOLBE.

In den elektronenmikroskopischen Arbeiten über Diatomeenmembranen, die erfreulicherweise in der letzten Zeit häufiger werden, herrscht keine Einheitlichkeit in den Bezeichungen der anatomischen Einzelheiten der Kieselmembran. Ich benutze in der vorliegenden Arbeit die nachstehenden Bezeichungen und schlage sie zur allgemeinen Benutzung vor.

Die Kammer (eine Definition dieser alten Bezeichnung erübrigt sich wohl) wird begrenzt: von den

Seitenwänden (dies sind die Wände, die die Kammern gegeneinander abgrenzen) und den

Aussenwänden. Eine Aussenwand schliesst die Kammern gegen das Zellinnere, die andere gegen die Aussenwelt ab.

Die eine Aussenwand wird gebildet durch oder trägt stets die

Siebmembran, ein dünnes, mit Poren oder Poroiden versehenes Kieselhäutchen. Auch die Gürtelbänder tragen Siebmembranen (ob immer?).

Die andere Aussenwand kann überhaupt fehlen, wie im Falle der „offenen Kammern" (s. unten). Falls vorhanden — bei allen „halbgeschlossenen Kammern" (s. unten) — trägt sie stets einen offenen Porus und wird als

Porenmembran bezeichnet.

Man kann verschiedene Kammertypen unterscheiden. Ich schlug (1948) die folgenden Bezeichnungen vor:

[1] Vergl. Elektronenmikr. Unters. etc. I: Ark. f. Bot. Bd. 33 A. No. 17. 1948.

1. Offene Kammern I Ordnung (Siebmembran mit einfachen Poren);
2. Offene Kammern II Ordnung (Siebmembran mit sekundären Kammern);
3. Halbgeschlossene Kammern I Ordnung (Siebmembran mit einfachen Poren);
4. Halbgeschlossene Kammern II Ordnung (Siebmembran mit sekundären Kammern).

Betreffs näherer Einzelheiten über diese Kammertypen verweise ich auf die zitierte Arbeit (Kolbe 1948, S. 6 ff.).

Pleurosigma aestuarii Bréb.

Taf. I, Fig. 1 und 2.

Bereits in den Jugendtagen der Elektronenmikroskopie veröffentlichten Müller und Pasewaldt (1942) eine Anzahl z. T. vorzüglicher Elektronenaufnahmen der Schalen von *Pleurosigma angulatum*. Die wesentlichsten Schlussfolgerungen, welche die Verfasser aus ihren Aufnahmen und Beobachtungen zogen, lassen sich wie folgt kurz zusammenfassen:

1. Die verkieselte Zellwand von *Pl. angulatum* zeigt einen deutlichen Kammerbau; die gewölbeartigen hexagonalen Kammern sind gegeneinander nicht durch Nachbarwände abgegrenzt, sie sind vielmehr kommunizierend und deren Aussenwände sind voneinander durch Kieselsäulen abgestützt bezw. auseinandergehalten. Zu der letzteren Auffassung gelangten die Verff. nachdem sie die Kieselschalen einer Wärmebehandlung unterzogen, welche die Aussenwände z. T. zusammensintern liess.
2. Die eine der beiden Aussenwände der einzelnen Kammern besteht aus einer Kieselhaut, die ein elliptisches Fenster besitzt. Dieses Fenster ist von einer dünnen Kieselmembran verschlossen, welche von kleinsten Poren oder Poroiden durchsetzt ist und von den Verfassern als Feinsiebmembran bezeichnet wird. Den Durchmesser der Poren geben die Verff. mit 3 mμ an — es handelt sich also um Gebilde, deren Grössenordnung bereits an der Grenze des Auflösungsvermögens des Elektronenmikroskops steht.
3. Die andere Aussenwand der Kammern ist ebenfalls eine dünne Membran, in der ein schmaler Schlitz in Richtung der Apikalachse der Zelle verläuft und die Kammer in ihrer ganzen Länge durchsetzt.

Gegen die Deutung von Müller und Pasewaldt wendet sich Hustedt (1945). Seine Kritik richtet sich insbesondere auf die Punkte 1 und 3. Nach seiner Meinung sind die Kammern — in Übereinstimmung mit dem allgemeinen Bauplan der Diatomeen — nicht kommunizierend, sondern durch feste Wände gegeneinander abgegrenzt. Die Kieselschalen, wie sie von Müller und Pasewaldt abgebildet werden, würden allen bisherigen Beobachtungen widersprechen und einen merkwürdigen Ausnahmefall darstellen. Ebensowenig glaubhaft und nicht mit unseren bisherigen Kenntnissen vereinbar erscheinen Hustedt die Schlitze (Punkt 3) und er erklärt diese auf den Abbildungen von Müller und Pasewaldt für Beugungsbilder. Hustedt will die Deutungen der genannten Verfasser nicht endgültig bestreiten, sondern nur seine Bedenken äussern und zu Diskussionen und Paralleluntersuchungen auffordern.

Ich muss gestehen, dass nach Betrachtung der technisch vollkommenen Bilder von Müller und Pasewaldt mir die gleichen Bedenken kamen, wie Hustedt. Insbesondere erschien mir die von den Verff. angewandte Hitzebehandlung (bis zum Zusammensintern der dünnsten Membranen) als ein sehr rohes Verfahren, das nur zu leicht zu Artefakten führen kann. Bestärkt wurde ich dadurch, dass die Aufnahmen von Müller und Pasewaldt, die ohne vorherige Hitzebehandlung erfolgten (z. B. ihre Fig. 5 a), nichts von dem Säulencharakter erkennen lassen, den ihre Fig. 7 (nach Anschmelzen der Schalen) zeigt.

Auch die merkwürdige Schlitzbildung bei einer der Kammer-Aussenwände stellt ein Novum dar und forderte zur Skepsis auf. Da die Breite der Schlitze jedoch schon in das Bereich der kleinsten Dimensionen hinabführt, konnte man die Existenz der Schlitze nicht ohne weiteres abweisen und sie als optische Artefakte erklären. Hustedt dürfte in seiner Behauptung zu weit gegangen sein, wenn er (l. c. S. 322) schreibt:

„Die schlitzförmigen Öffnungen der einen Membranfläche sollen eine Länge von etwa 0,6 μ und eine Breite von 0,03 μ haben, derartige ‚Risse' in einer dünnen Zellwand würden sich aber mit Hilfe unserer Apochromate und bei Anwendung stark brechender Einschlussmittel unbedingt auch durch subjektive Beobachtung im Lichtmikroskop feststellen lassen (bei *Amphipleura pellucida* und bei *Frustulia rhomboides* var. *saxonica* beträgt der Durchmesser der Strukturelemente nur etwa 0,25 μ, bei anderen Arten sind sie noch zarter, trotzdem unter günstigen Bedingungen noch auflösbar), zumindest müssen sich bei subjektiver Beobachtung zarte Längslinien ergeben, von denen etwa 50 auf 10 μ kommen."

Diese Schlussfolgerung ist nicht zwingend, denn ein langgestrecktes Gebilde, dessen Breite weit unter der lichtmikroskopischen Sichtbarkeit liegt (0,03 μ!) ist im Lichtmikroskop bestimmt nicht sichtbar, selbst wenn dessen Länge relativ gross ist; ob ein Gitter aus solchen Gebilden optisch sichtbare Beugungsbilder ergeben kann (wie dies HUSTEDT wohl mit seinem letzten Satz meint), dürfte physikalisch eine offene Frage sein. Ein Beispiel bilden unsichtbare lange Viren und die längsten Kettenmoleküle, die oft eine relativ bedeutende Länge aufweisen können bei einer submikroskopischen Breite. Aber abgesehen von theoretischen Erwägungen bekam ich bei elektronenmikroskopischen Untersuchungen zuweilen *Pleurosigma*- oder *Gyrosigma*-Schalen zu Gesicht, die schlitzförmige Bildungen zeigten. Jedoch waren die Bilder nicht überzeugend, vor allem weil infolge der Dicke der Schalen die Kammern für den Elektronenstrahl nicht genügend durchlässig waren.

Ich suchte daher nach einem geeigneten dünnwandigen Vertreter der Gattung *Pleurosigma*, dessen Häufigkeit im Material genügte, um eine elektronenmikroskopische Untersuchung zu ermöglichen. Vor einiger Zeit erhielt ich von Herrn JEAN LÉPINE, Reims, eine Probe von *Pleurosigma aestuarii* Bréb. und ich möchte an dieser Stelle Herrn LÉPINE herzlich danken für die freundliche Überlassung seines Materials. Diese Form erwies sich günstiger in elektronenmikroskopischer Beziehung, als *Pl. angulatum*, infolge ihrer Zartheit.

Die elektronenmikroskopischen Aufnahmen von *Pl. aestuarii* (Taf. I, Fig. 1 u. 2) lassen die gleiche Schalenstruktur erkennen, wie *Pl. angulatum*. In Fig. 1 kann man jedoch die Seitenwände in ihrem ganzen Verlauf recht gut verfolgen. Man erkennt, dass diese Wände durchlaufend sind, wenn auch ihre Kreuzungsstellen (bezw. die Stellen, an denen 2 Wände zusammenstossen) Verdickungen aufweisen. Man erkennt ferner deutlich die ovalen Fenster einer der Aussenwände; die Siebmembran ist — wie so häufig bei längerer Lagerung des Materials in wässrigen Medien — leider restlos aufgelöst. Doch ist dies für die Fragen, die hier diskutiert werden sollen, nicht von wesentlicher Bedeutung.

Die andere Aussenwand (ob dem Zellinneren oder der Aussenseite der Zelle zugekehrt, liess sich hier nich nachweisen) zeigt deutlich die Schlitze, die die Kammermembran in apikaler Richtung durchsetzen. Besonders instruktiv ist die Betrachtung der Bruchkante der Schale auf Fig. 1. Hier tritt an einigen Stellen (z. B. am

hervorstehenden Bruchrand rechts) infolge Abbrechens der einen Kammer-Aussenwand die „Schlitzmembran" frei in den Raum hinein. An diesen Stellen, an denen der Schlitz oder dessen Teile sichtbar werden, zeigt es sich, das der Schlitz bezw. dessen Wände wirkliche, reale Gebilde sind.

Zu den anfangs zitierten Streitfragen möchte ich daher wie folgt Stellung nehmen:

1. Die Seitenwände der Kammern von *Pl. aestuarii* (und wohl auch bei den anderen *Pleurosigma*-Arten), welche die Aussen- und Innenmembran verbinden, sind fortlaufende, vollständige Wände, wie dies bereits Hustedt annahm.
2. Die Schlitze der einen Aussenwand sind reale Gebilde, es sind schmale Spalte in einer dünnen Kieselmembran und durchsetzen die Kammer apikal in ihrer ganzen Länge.

Die Kammern der *Pleurosigma*-Zellwand erscheinen mithin als Raumgebilde von hexagonalem Querschnitt, die gegeneinander durch feste Wände getrennt sind, ähnlich aneinandergekitteten sechseckigen Schachteln. Den Deckel der Schachteln bildet einen Kieselmembran, die ein elliptisches „Fenster" besitzt, über das eine Siebmembran mit zahlreichen Poren oder Poroiden gespannt ist. Der Boden der Schachteln (die andere Aussenwand der Kammern) ist ebenfalls von einer Kieselmembran gebildet, welche bei dieser Gattung von einem schmalen parallelrandigen Schlitz durchzogen ist. Dieser Kammertypes entspricht dem Schema 3: halbgeschlossene Kammern I Ordnung. Die einzige Abweichung von den bisher bekannten Kammern besteht darin, dass der „Boden" der Kammern nicht ganz offen oder durch einen ± grossen Porus mit der Aussenwelt kommuniziert, sondern einen Schlitz trägt. Der Schlitz ist allerdings ein Novum, das erst durch das Elektronenmikroskop erschlossen worden ist.

Übrigens ist die Schlitzbildung nicht nur auf die Gattung *Pleurosigma* (und sicher auch *Gyrosigma*) beschränkt, sondern findet sich wahrscheinlich auch bei Gattungen, die durch einen ähnlichen Streifentypus (im lichtmikroskopischen Sinne) ausgezeichnet sind, z. B. in der Cleve'schen Gruppe der *Naviculae orthostichae*. Für *Navicula crucigera* (W. Sm.) Cl. hat dies N. Ingram Hendey nachweisen können. Herr Hendey hat mir freundlichst erlaubt seine bisher unveröffentlichte ausgezeichnete Aufnahme (Taf. II, Fig. 3) hier zu benutzen, wofür ich ihm auch an dieser Stelle meinen

wärmsten Dank ausspreche. Die Aufnahme zeigt genau die gleiche Schlitzbildung, wie wir dies bei *Pleurosigma* sahen; die Kammern sind jedoch — entsprechend dem Streifungstypus — hier rechteckig.

In Fig. 2 (Taf. I) ist das Schalenende von *Pleurosigma aestuarii* abgebildet. Es ist interessant, dass im oberen Teil die *Pleurosigma*-Struktur unvermittelt in eine *Gyrosigma*-Struktur übergeht (Streifensysteme, die sich im rechten Winkel schneiden). Entsprechend geht der Kammerquerschnitt vom sechseckigen Typus zum viereckigen über, wie man ihn auch bei HENDEYS Aufnahme beobachten kann. An einigen Teilen der Aufnahme (Fig. 2) sieht man eine Verschiebung der Schlitze aus ihrer medianen Lage gegenüber der Kammerachse. Dies beruht auf der ziemlich starken Krümmung der Schale an den Zellenden; wegen der grossen Tiefenschärfe des Elektronenmikroskops ist jedoch diese Krümmung auf dem Bild nicht erkennbar, während die Schlitze infolge der Krümmung in parallaktischer Verschiebung erscheinen.

Anomoeoneis (Navicula) subtilissima Cl.

Taf. I, Fig. 4; Taf. II, Fig. 5, 6.

Die Struktur von *Navicula subtilissima* wird bekanntlich im Lichtmikroskop nur unter den besten Bedingungen mit Mühe und auch dann nur höchst unvollkommen aufgelöst. Unter dem Elektronenmikroskop erweist es sich, dass die Striae nicht kontinuierlich, sondern in einige mehr oder weniger lange Teilstücke aufgelöst sind. Jedes Teilstück stellt eine $\pm$ lange offene Kammer dar (Typus 1 — offene Kammern I Ordnung), deren Boden, wie wohl stets, aus einer Siebmembran besteht. Die Siebmembran (vgl. Fig. 6) hat in diesem Fall feine Poren (oder Poroiden), deren Durchmesser etwa zwischen 4 und 6 mμ schwankt; interessant sind die kurzen Leisten, die von den Kammerwänden auf die Siebmembran übergehen. Sie konnten auch bei einigen anderen Formen nachgewiesen werden und eine Siebmembran von diesem Typus bildet einen Übergang zum Kammertypus 2: Offene Kammern II Ordnung.

Das Interessanteste der Aufnahme ist jedoch die Art der Streifung: diese unterbrochenen, zerrissenen Striae, „. . . wellige Längslinien bildend, die durch mehr oder weniger ausgedehnte hyaline Streifen voneinander getrennt sind" (HUSTEDT 1930, S. 261) sind ausserordentlich charakteristisch für *Anomoeoneis*-Arten, besonders für die kleinen Formen. Auch die marginalen Längslinien fehlen

nicht, wie alle 3 Figuren zeigen. Vergleicht man die hier dargestellte Streifung von *Navicula subtilissima* mit den elektronenmikroskopischen Aufnahmen von *Anomoeoneis serians* var. *brachysira* und *A. follis* (Kolbe u. Götz 1943, S. 95, Taf. III, Fig. 9 und 10), so drängt sich die Ähnlichkeit förmlich auf. Man vergleiche aber auch die „normalen" Zeichnungen, z. B. von Hustedt (1930) von *Anomoeoneis exilis, styriaca, follis.*

Ich zweifle daher nicht, dass man richtiger tut, *Navicula subtilissima* zur Gattung *Anomoeoneis* zu stellen. Die kleinen hyalinen Formen mancher Naviculaceen lassen sich lediglich auf Grund ihrer Umrissform, ihrer kaum angedeuteten Struktur und eventuellen anderen wenig ausgeprägten Kennzeichen nur sehr unsicher in eine der bestehenden Gattungen einordnen. In solchen Fällen kann das Elektronenmikroskop eine wertvolle Hilfe für die Taxonomie ergeben.

Auf dem Internationalen Botanischen Kongress in Stockholm wurde bei einer Gelegenheit die Frage über den Wert des Elektronenmikroskops im Dienst der Systematik aufgeworfen. Die Taxonomen verhielten sich skeptisch und das bestimmt mit einem gewissen Recht: es ist wohl kaum anzunehmen, dass das Elektronenmikroskop in absehbarer Zeit die Rolle des Lichtmikroskops übernehmen wird und laufende Untersuchungen mit diesem Instrument vorgenommen werden können. Sogar die Nachprüfung kritischer Formen (besonders seltener) ist infolge der besonderen Technik des Instruments nur in seltenen Fällen möglich. Man wird zunächst also mehr auf Zufallsergebnisse angewiesen sein. Sind diese aber von taxonomischem Wert, so sollten einsichtige Systematiker sich diesen Resultaten nicht verschliessen, wenn sie sonst in keinem Widerspruch mit übergeordneten systematischen Gesichtspunkten stehen. Und dies wird bei den kleinen Formen mit kaum erschlossener Struktur wohl nie der Fall sein.

Nitzschia sp.

Taf. IV, Fig. 8 und 9.

Um die Aufnahme Fig. 9 richtig zu verstehen, muss man sich zunächst über den Aufbau dieser *Nitzschia*-Schale an Hand des Schemas Taf. IV, Fig. 8 orientieren. Fig. 8 a zeigt perspektivisch die dachfirstähnliche Schale, deren Firstkante vom Kiel gebildet wird. Unterhalb des „Firstes" sieht man eine trägerartige Membranleiste

mit ausgesparten fensterartigen Öffnungen, die äusserste Schalenkante gegen das Zellinnere abschliesst; das Ganze — Schalenkante, Leiste und Kiel — ist eine Art primitiver Kanalraphe, wie sie von HUSTEDT (1928, 1929) für einige Gattungen beschrieben wurde. Auf die Bedeutung dieser eigenartigen Bildung komme ich später zurück. Fig. 8 b zeigt schematisch dieselbe Schale, wie Fig. 8 a, jedoch in der Lage, in welcher sich das photo- (richtiger: elektro-) graphierte Exemplar befindet, das um 180° gedreht ist und dem Beschauer die Innenseite der Schale zuwendet.

In der Elektronenaufnahme Fig. 9 ist die Leiste in grosser Schärfe zu sehen; die Fenster in der Leiste erscheinen als ausgesprochene Öffnungen; unter ihnen verlaufen (etwas heller) die Ränder des Kiels. Median zwischen den Kielrändern erscheint der Raphenspalt; er ist auf dem Originalabzug deutlich sichtbar, wurde jedoch bei der Reproduktion undeutlich.

Es empfiehlt sich, zum besseren Verständnis die vorliegende Abbildung mit einer früher veröffentlichten Stereoaufnahme (KOLBE u. GÖLZ 1943, Taf. IV, Fig. 22 a/b) zu vergleichen. Betrachtet man diese mit dem Stereoskop, so kann man die Lage der Leiste im Raum sehr deutlich erkennen; ferner sieht man — was für die späteren Ausführungen von Bedeutung ist — dass die Leiste eine flache Membran ist. Endlich ist in dieser Aufnahme der Raphenspalt klar abgebildet.

Die Diatomologen haben sich seit langem damit beschäftigt, die Entwicklung der Raphe — von der Raphe der Naviculaceen zur hochentwickelten Flügelraphe der Surirellaceen — zu verfolgen. Von den älteren Autoren abgesehen, deren zeitgenössische Instrumente genauere Untersuchungen dieser in optischer Hinsicht sehr schwierigen Materie kaum zuliessen, ist ein grosser Fortschritt seit den Arbeiten von O. MÜLLER und F. HUSTEDT zu verzeichnen. HUSTEDT gebührt entschieden das Verdienst, die ersten Ansätze zu einer Kanalraphe bei den Gattungen *Epithemia*, *Denticula*, *Hantzschia* und *Nitzschia* weitgehend geklärt zu haben. MÜLLER (1898) hat in der Raphenfurche von *Epithemia* bereits helle Tüpfel wahrgenommen, gezeichnet (l. c. Taf. XXVI, Fig. 1), aber im Text nicht diskutiert. HUSTEDT (1928, 1929) hat diese Tüpfel bei einer Anzahl Gattungen eingehend studiert und sie mit der Ausbildung bezw. Entwicklung der Raphe zur Flügelraphe in Zusammenhang gebracht. Bei der Schwierigkeit lichtoptischer Untersuchung dieser feinen Gebilde konnte HUSTEDT noch nicht absolut sicher sein, ob es sich tatsächlich um

durchgehende Öffnungen handelte, vermutete es aber, wenn er vorsichtig schreibt (HUSTEDT 1928, S. 155): „. . . halte ich es für möglich, dass die Flecke unter der Raphe nicht nur Tüpfel, sondern regelrechte Öffnungen im Kanalmantel darstellen, die die Bildung von Kielpunkten und Flügelkanälen einleiten würden!". Unsere Abbildung 9 zeigt nun objektiv und mit aller Deutlichkeit, dass HUSTEDT Recht hatte und dass die Poren der Membranleiste unter dem Kielspalt tatsächlich Öffnungen darstellen.

Bei der hier abgebildeten *Nitzschia* ist die Entwicklung zur Flügelraphe noch nicht sehr weit gediehen. Man könnte sich diese Entwicklung mit HUSTEDT ungefähr so denken, dass zunächst die Raphe vom Typus der Naviculaceen mehr und mehr an die Schalenkante vorrückt. Dann wird die Schalenkante durch eine mit Fenstern versehene Innenleiste teilweise gegen das Zellinnere abgegrenzt. Gleichzeitig ändert sich der Charakter der Raphe: unter Erhöhung der raphetragenden Schalenkante zu einem Kiel wird der äussere Raphespalt zum Kielspalt und die Rolle des inneren Raphespalts übernehmen die Öffnungen der Innenleiste (dies würde dem Stadium entsprechen, auf dem sich die hier abgebildete *Nitzschia* befindet). Der vom übrigen Zellkörper abgetrennte Raum zwischen Kiel und Innenleiste entwickelt sich zu einem spalttragenden Rohr, das über die Schalenkante weiter emporgehoben wird (Flügel) und die Leistenöffnungen werden zu Flügelkanälen — ein Endstadium, das von den Surirellaceen erreicht wird.

Dies ist in sehr groben Zügen der Entwicklungsgang der Flügelraphen der Surirellaceen; auf diesem Wege stellen die *Nitzschia*-Raphen ein Zwischenstadium dar. Die Entwicklung ergibt sich aus den Untersuchungen HUSTEDTS, der sie genau beschrieb. Der Raum gestattet es nicht, auf weitere wichtige Einzelheiten einzugehen und ich verweise auf die diesbezüglichen Originalarbeiten HUSTEDTS. Es kam mir an dieser Stelle darauf an, auf die Identität der elektronenmikroskopischen Bilder mit den Darstellungen HUSTEDTS hinzuweisen. Man vergleiche z. B. seine Abbildungen (1928, Taf. III, Fig. 8, 10, 11) mit der vorliegenden Fig. 9! Die Stereoskopaufnahme von 1943 ergänzt das Bild zu einem Raumbild. Die elektronenmikroskopischen Aufnahmen bilden mithin, wie so häufig, eine objektive Bestätigung, die umso wichtiger ist, je schwieriger die lichtmikroskopische Auflösung und Deutung feinster Strukturen wird.

TOMAN und ROSZIVAL (1948) untersuchten besonders *Nitzschia amphibia* und *N. Hantzschiana* und fanden ebenfalls eine mit Poren

versehene Innenleiste, wie sie bei KOLBE u. GÖLZ (1943, Taf. VI, Fig. 22 a/b) räumlich dargestellt ist. Die Verff. erwähnen auch, dass es ihnen gelang, Mittel- und Endknoten bei den genannten Formen nachzuweisen. In ihrer Aufnahme Fig. 4, auf die es hier besonders ankommt, lässt sich über die Lage der Innenleiste im Zellraum schwer etwas Sicheres aussagen, ebenso erkennt man darin nicht die Mittel- und Endknoten. Jedenfalls haben die Verff. die Gegenwart der Innenleiste zweifellos nachgewiesen und lieferten somit eine weitere Bestätigung für die Richtigkeit der Deutung HUSTEDTS. In dem Schema der Kielstruktur (l. c. S. 29) bilden sie im Kielraum grosse seitliche Fenster ab; solche Bildungen habe ich nie beobachten können. Sie sind — wenigstens theoretisch — schwer erklärlich und gehen aus ihren Aufnahmen auch nicht ohne Weiteres hervor. Die Verff. entwickeln ferner an Hand ihrer Aufnahmen (l. c. Fig. 1 bis 3) den Werdegang der allmählichen Verkieselung der Zellmembran. Solche Bilder habe ich bei anderen Diatomeen oft gesehen. Ich deutete sie als Korrosionserscheinungen, da sie besonders häufig zu finden waren bei toten Zellen, die längere Zeit mit wässrigen Medien in Berührung standen. Die Frage, ob es sich in den von den Verff. beschriebenen Fällen um Entwicklungs- oder Korrosionsstadien handelt, dürfte ohne weitere kritische Untersuchungen kaum zu entscheiden sein.

Amphipleura pellucida Ktz.

Taf. IV, Fig. 7.

Anhangsweise soll noch dieses berühmte Testobjekt kurz erläutert werden. *Amphipleura pellucida* bietet einige Schwierigkeiten auch für elektronenmikroskopische Aufnahmen, denn sie macht ihrem Artnamen „pellucida" wenig Ehre: sie ist ausgesprochen dickschalig und — für den Elektronenstrahl — wenig durchscheinend. Infolgedessen zeichnen sich die Kammern nur undeutlich durch die relativ dicken Aussenwände ab. In der Aufnahme Taf. IV, Fig. 7 ist eine Bruchkante aufgenommen, die immerhin einigen Aufschluss über die feinere Struktur von *A. pellucida* gibt.

Man sieht an einigen Stellen der Bruchkante, dass die Kammern relativ gross sind; sie sind nach der einen Aussenseite durch eine Siebmembran, nach der anderen durch eine Porenmembran geschlossen, die mit einem auffallend kleinen Porus versehen ist. Der

Kammerbau entspricht mithin dem Typus 3 (halbgeschlossene Kammern I Ordnung).

Der Durchmesser des Porus beträgt nur etwa 30 mμ, während die Kammern etwa 110 mμ weit ist. Die Siebmembran sieht man auf der Aufnahme nur andeutungsweise und auf der Reproduktion so gut wie garnicht. Sie scheint 2 längliche Poren (oder vielleicht sekundäre Kammern?) zu besitzen, zu deren Darstellung eine viel höhere Vergrösserung notwendig ist.

Es ist möglich, dass die beiden Momente: verhältnismässig dicke Aussenmembranen und submikroskopisch kleine Poren der Porenmembran auch die bekannt schwierige lichtmikroskopische Auflösung von *Amphipleura pellucida* bedingen. Wenn die Aussenwände für das sichtbare Licht auch unvergleichlich durchlässiger sind, als für den Elektronenstrahl, so dürfte die Tatsache bestehen bleiben, dass die Dicke dieser Membranen den Lichtkontrast zwischen den dicken Kammer-Seitenwänden und dem Kammerinneren abschwächen. Und auf diesen Kontrast beruht wohl zum grossen Teil die lichtoptische Auflösbarkeit feinster Strukturen.

Die elektronenmikroskopischen Arbeiten wurden im Karolinska Institutets avdelning för cellforskning, Stockholm, ausgeführt und es ist mir eine angenehme Pflicht, Herrn Professor Caspersson verbindlichst zu danken, dass er mir gestattete, die Hilfsmittel seines Instituts zu benutzen. Ich erfreute mich bei meinen Arbeiten der wertvollen und liebenswürdigen Hilfe von Herrn Professor Fernández-Morán, dem ich auch an dieser Stelle dafür herzlichst danken möchte. Mein bester Dank gebührt ferner Herrn Professor Hultén, der mir einen Arbeitsplatz in der botanischen Abteilung des Riksmuseum freundlichst überliess.

Stockholm, Botanische Abteilung des Riksmuseum, Oktober 1951.

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Fig. 1.

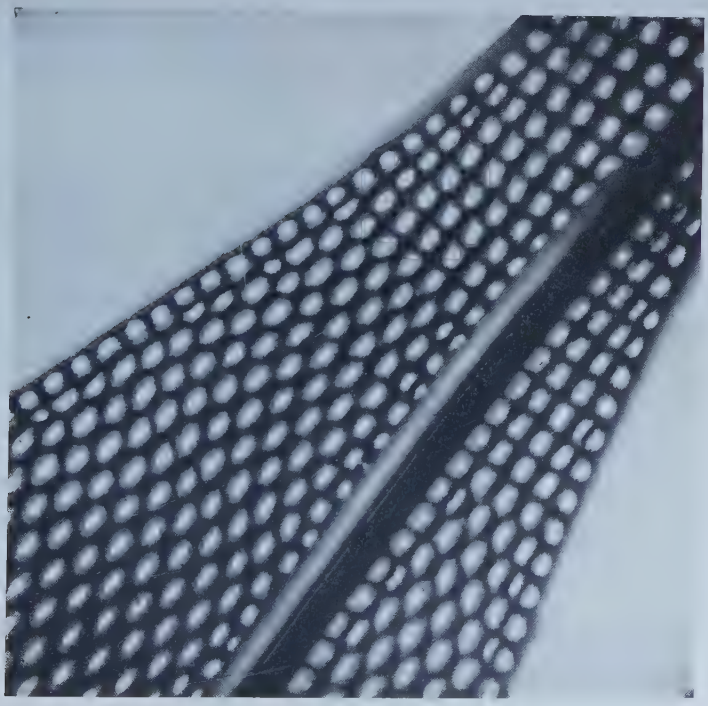

Fig. 2.

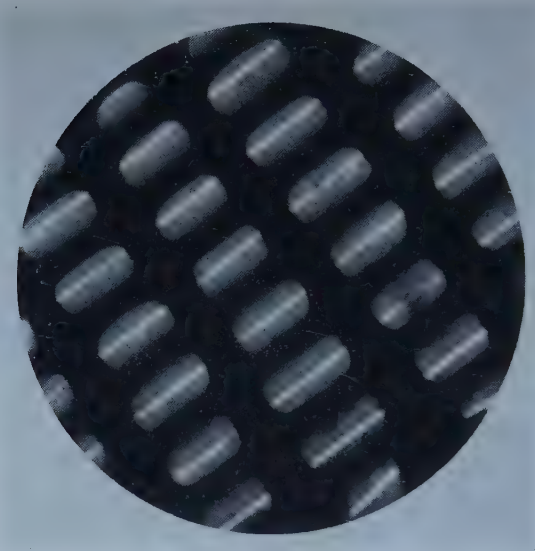

Fig. 3.

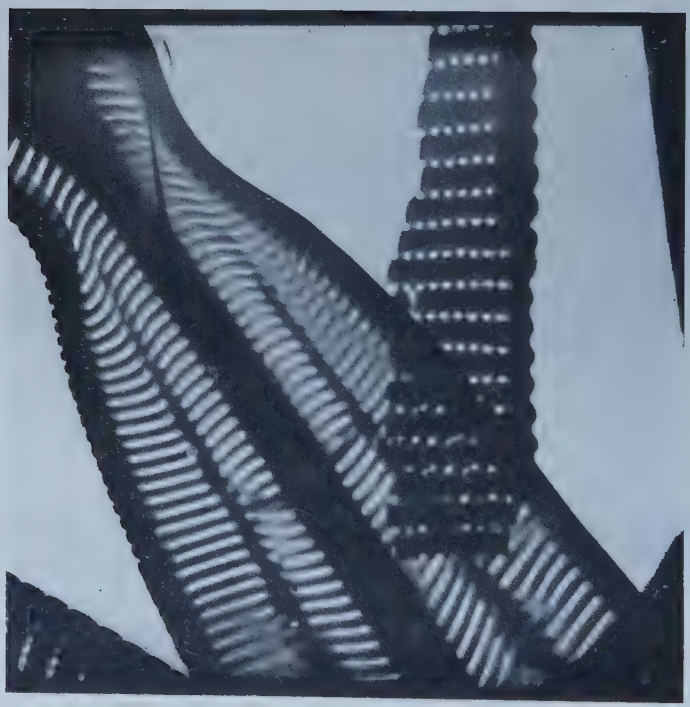

Fig. 4.

Fig. 5.

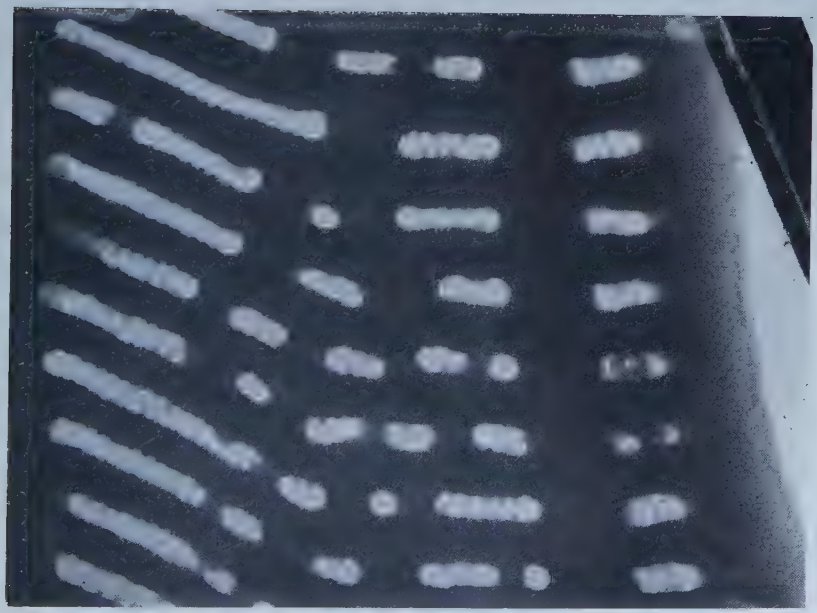

Fig. 6.

Fig. 7.

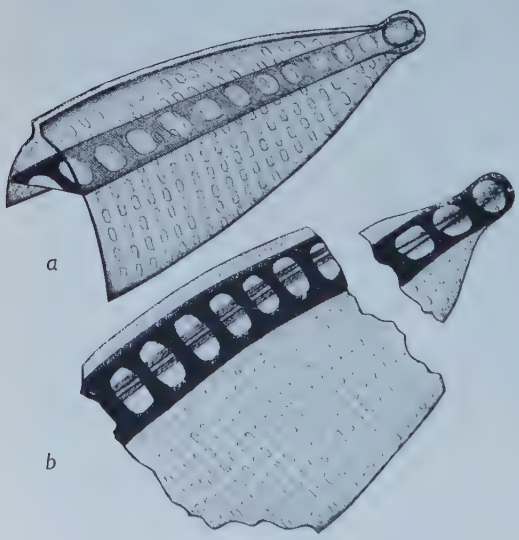

Fig. 8.

Fig. 9.

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Toman, M. and Roszival, M., 1948: The structure of the Raphe of *Nitzschiae*. — Studia Botanica Čechoslovaca, Vol. 9. Fasc. 1. Praha.

Erläuterungen zu den Tafeln.

Die Aufnahmen wurden zum grossen Teil mit einem amerikanischen Elektronenmikroskop im Karolinska Institutets avdelning för cellforskning (Prof. Caspersson) gemacht (Fig. 1, 2, 4, 5, 6) mit einer Elektronenenergie von etwa 40 kV. Zu den Aufnahmen 7 und 9 wurde das elektrostatische Übermikroskop des A. E. G.-Forschungsinstituts in Berlin verwandt mit einer Elektronenenergie von 50 kV. Die Aufnahme Fig. 3 wurde von N. Ingram Hendey in England gemacht und mir freundlichst zur Verfügung gestellt. Alle Aufnahmen wurden photographisch nachvergrössert, damit die Einzelheiten bei der Reproduktion nicht verloren gingen.

Die Vergrösserungszahlen bedeuten die Gesamtvergrösserung und sind ungefähr.

Tafel I.

Fig. 1. *Pleurosigma aestuarii* Bréb. Mittlerer Teil eines Schalen-Bruchstücks ..... 18 000 : 1
Fig. 2. Dieselbe, Schalenende ..... 10 000 : 1

Tafel II.

Fig. 3. *Navicula crucigera* (Gr.) Cl. Mittlerer Teil einer Schale. Aufnahme N. I. Hendey ..... 17 000 : 1
Fig. 4. *Navicula subtilissima* Cl. Kopfende ..... 12 000 : 1

Tafel III.

Fig. 5. *Navicula subtilissima* Cl. Mittlerer Teil der Schale ..... 15 000 : 1
Fig. 6. Dieselbe Ausschnitt, stärker vergrössert ..... 33 000 : 1

Tafel IV.

Fig. 7. *Amphipleura pellucida* Ktz. Bruchstück einer Schale (die helleren Bruchkanten gehören der das Objekt tragenden dünnsten Collodionmembran) ..... 20 000 : 1
Fig. 8. Schema zu Fig. 9. Erklärung im Text.
Fig. 9. *Nitzschia* sp. auf dem Kiel liegend. Man beachte den (auf der Reproduktion schwer sichtbaren) Raphenspalt. ..... 7 500 : 1

Svensk Botanisk Tidskrift. Bd 45, H. 4. 1951.

THE EFFECT OF TEMPERATURE, pH AND MALT EXTRACT UPON GROWTH AND PERITHECIAL DEVELOPMENT OF TWO GNOMONIA SPECIES.

BY

LARS ERIC HENRIKSSON and JOHN F. MORGAN-JONES.

Introduction.

The genus *Gnomonia* comprises a small number of leaf-inhabiting, non-stromatic pyrenomycetes, of the Order *Sphaeriales*. It is cosmopolitan in distribution, as shown by the following references: Bermuda: Seaver & Waterston (1940); Brazil: Arruda (1946); Greenland: Lind (1926); Japan: Matsumoto (1931); New Zealand: Murray (1926); Sweden: Lind (1928); U. S. A.: Alexopoulos & Cation (1948) etc.

With the exception of the various floras, references to *Gnomonia* in the literature are relatively few, most of them being confined to short, phytopathological descriptions. Only three cytological works have been published on the genus (Brooks, 1910; Likhité, 1926; Pomerleau, 1938), and nothing on its physiology.

Several species of *Gnomonia*, collected in the woods about Uppsala, have been isolated in pure culture (Morgan-Jones, unpublished). Two of these, *Gnomonia vulgaris* Ces. et de Not. on *Corylus avellana* and *Gnomonia intermedia* Rehm. on *Betula pubescens*, were chosen for the investigation, since their rapid growth rate, as well as their readiness to form perithecia upon artificial media, made them ideally suited to cultural studies.

A cytological investigation is presently being carried out by Morgan-Jones, and an investigation into the nutrient requirements of the genus by Henriksson.

The present work was undertaken jointly by the authors in an effort to throw some light on the basic physiology of the fungus.

Perithecia appear generally in late autumn, on the underside of dead, freshly-fallen leaves. The basal spherical portion, partially or entirely covered by the epidermis, is surmounted by a long, projecting neck (Figs. 1 and 2). Perithecia may occur on the laminae, veins and petioles, or may be restricted to one or the other of these places, according to the species.

Isolation and Culture.

An individual perithecium was surface-sterilized by the hypochlorite method of Wilson (Melin, 1939), washed in two changes of sterile water and crushed in one ml. of sterile water. The resulting suspension of asci and free ascospores was transferred by means of a sterile micropipette to petri dishes containing Leonian's agar, the cultures being stored in a thermostat at 20° C. Under such conditions, the ascospores germinated usually within 12 hours, mycelial growth becoming visible to the naked eye after about three days.

Since Leonian's agar was found to favour both vegetative growth and perithecial development, it has been used throughout the investigation, either in its original form or slightly modified. Its composition is as follows: $KH_2\ PO_4$, 0.125 gm.; $MgSO_4 \cdot 7\ H_2O$, 0.0625 gm.; peptone, 0.0625 gm.; maltose, 0.625 gm.; malt extract, 0.625 gm.; distilled water, 100 ml.; agar, 2 %.

The malt extract according to Liebig was from Vitrum, Sweden, and Witte Peptone from Schering-Kahlbaum. The salts were pro analysis.

Attempts to measure the amount of growth in terms of mycelial dry weight were unsuccessful since the mycelium, in fluid culture, failed to form a compact mat, e. g., of the *Aspergillus* type. It was considered that in a preliminary investigation such as this, a measure of the *relative growth rate* would be sufficient. The relative growth rate, an expression of the total increase in area of the entire colony, was calculated by the formula $\pi \cdot (R^2 - r^2)$.

Agar pieces used for inoculating the series were of uniform size.

It should be emphasized that all cultures, immediately after inoculation, were left in the dark for 48 hours at room temperature (20° C), after which they were transferred to their respective thermostats, measures being taken to prevent the cultures from drying out. A minimum adaptation period of 48 hours was then allowed to elapse before the initial measurements of the colonies were made. This was done so that (a) cultures at the more extreme temperatures

Fig. 1. Young perithecia of *G. intermedia* on agar. (42 ×).

Fig. 2. Cross section of one of the perithecia in Fig. 1, showing the spherical body, long beak-like neck and central core of immature asci. (173 ×). — Photo ELISABET HENRIKSSON.

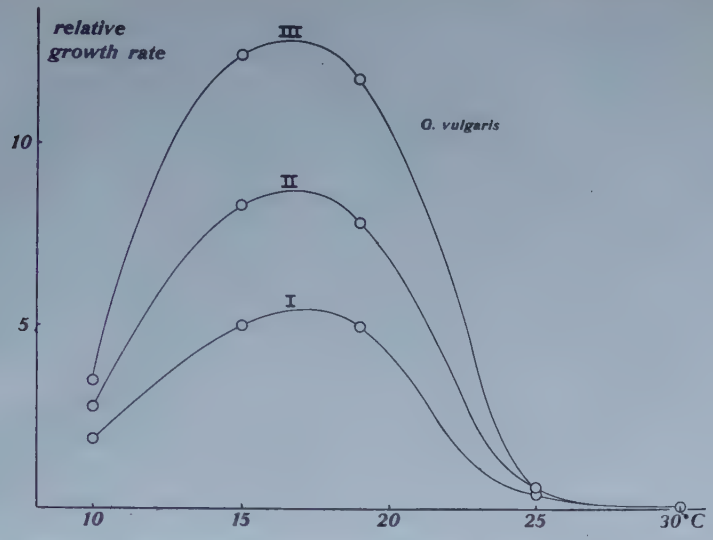

Fig. 3. Effect of temperature on *Gnomonia vulgaris*. (72 hours between each curve).

would have time to adjust themselves to their new temperature environment, and (b) so that the colonies would have attained a measurable size. In the case of *G. intermedia*, this size was reached by the end of 48 hours. Cultures of *G. vulgaris* grew more slowly, a fact which will be specified in the text.

All measurements were made during the early period of growth, i. e., while the cultures were symmetrical. Cultures were maintained in darkness throughout the experiments.

Effect of Temperature (Expt. 1).

(a) Vegetative growth.

Culture series of *G. intermedia* and *G. vulgaris* were placed in thermostats at 5°, 10°, 15°, 19°, 25°, 30°, and 35° C, respectively. The pH of the medium, after autoclaving, was 5.6.

Measurements of the *G. intermedia* series, begun at the close of the adaptation period, were continued at 36-hour intervals until the colonies showed signs of asymmetry. Results are illustrated in Fig. 4, curves I and II.

In the case of the slower-growing *G. vulgaris*, colonies had not attained a measurable size until a week after inoculation. Three measurements were made at corresponding 72-hour intervals. Results are shown in Fig. 3.

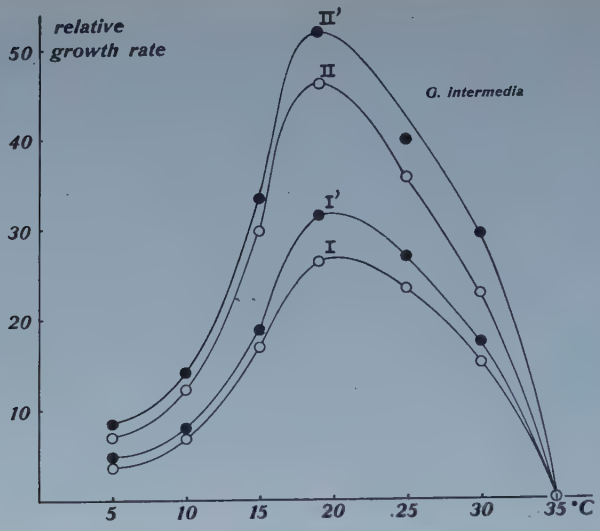

Fig. 4. Effect of temperature on *Gnomonia intermedia*. (36 hours between Curves I and II, and between I' and II'). Curves I' and II', see Expt. 3.

A comparison of curves I and II in Fig. 4 with those in Fig. 3 indicates that the temperature-growth range of *G. intermedia* is greater than that of *G. vulgaris;* for while growth in the case of *G. vulgaris* ceases at 30° C., that of *G. intermedia* does not cease until a temperature of 35° C has been reached.

The optimum temperature for *G. vulgaris* appears to be about 17° C., that of *G. intermedia* about 19° C.

(b) **Perithecial development.**

After measurement, cultures of both series were left in their respective thermostats and examined daily for signs of perithecial development.

Eighteen days after inoculation, young perithecia of *G. vulgaris* had become visible in the 15° C cultures. In the case of *G. intermedia*, fruiting was slower; not until 30 days after inoculation did the first perithecia appear in the 19° C cultures. Thus, not only does perithecial development appear to be more rapid in the case of *G. vulgaris*, but it seems to be favoured by a slightly lower temperature. This fact is illustrated in Plates I and II and in Table I. In Table I, the degree of perithecial development was measured directly by counting the number of fruit bodies per plate. The authors realise

Table I. Effect of temperature on perithecial development of *Gnomonia intermedia*. Values indicate the maximum number of fruit-bodies per plate, 60 days after inoculation.

Medium \ Temp. °C	5	10	15	19	25	30	35
Leonian's agar.							
Expt. 1 & 3	1	4	7	17	—	—	—
Leonian's agar mod.							
Expt. 3	33	66	115	114	—	—	—

that this also would have been desirable in the case of *G. vulgaris*, but was impossible, due to the tendency of the perithecia to clump.

Plates I and II seem to indicate that *G. vulgaris* forms perithecia within a relatively narrow temperature range, viz., minimum above 10° C, optimum 15° C, maximum between 19—25° C. On the other hand, it would appear from Table I that *G. intermedia* has a wider temperature range, perithecial development occurring at temperatures from 5° C to 19° C. It is interesting to note that in both species super-optimum temperatures produce a rapid cessation in perithecial development, neither species forming perithecia at or above 25° C.

Effect of pH (Expt. 2).

(a) Vegetative growth.

Leonian's agar was adjusted to various pH values by means of 0.1 M HCl and 0.1 M NaOH, the following series being obtained after autoclaving: 3.2, 4.3, 4.8, 5.2, 5.4, 5.7, 6.6, 7.1. Attempts to adjust Leonian's medium to pH values as high as 10.5 were unsuccessful, such values falling to about 7.0 during autoclaving.

Cultures of *G. vulgaris* and *G. intermedia* were maintained at 15° C and 19° C respectively, the relative growth rate being measured by the method previously described. Results are illustrated in Fig. 5. The curves seem to indicate that *G. vulgaris* has an optimum growth-pH of 5.4—5.7, the optimum growth-pH of *G. intermedia* being about 4.3 or a little lower. In contrast to *G. vulgaris* which refused to grow at pH values around 3, *G. intermedia* is more tolerant of an extremely acid medium. It also appears to survive better in an extremely high pH environment.

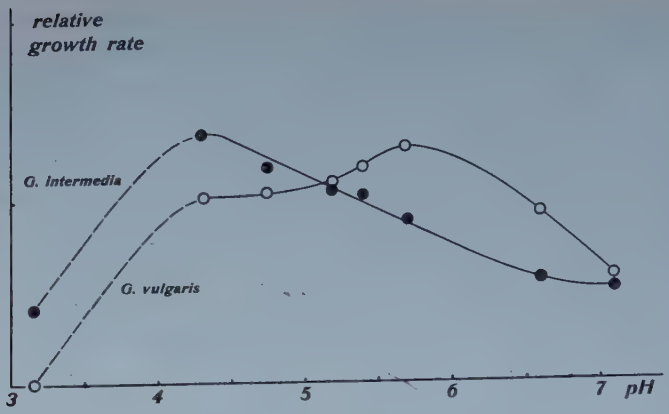

Fig. 5. Effect of pH on growth of *Gnomonia vulgaris* and *G. intermedia*.

(b) **Perithecial development.**

Fifteen days after inoculation, young perithecia of *G. vulgaris* had begun to form in all pH series except 3.2. The cultures were allowed to develop for an additional 10 days and then photographed. (Plates III and IV.) A careful examination of the cultures indicated that the greatest number of perithecia occurred at pH 5.2. Taking the series as a whole, the effect of different pH values on perithecial development may be summarized as follows:

$$7.1 < 6.6 < 5.7 \text{ and } 5.4 < 4.3 \text{ and } 4.8 < 5.2.$$

Fruit bodies of *G. intermedia* appeared 21 days after inoculation. After an additional developmental period of 15 days, a count was made in each series of the number of fruit bodies per plate. Unfortunately, the great variation between individual counts at pH values between 4.3 and 6.6 makes only a general statement possible, viz., that in the pH range 5.4—5.7, the number of perithecia per plate varied between 160 and 180. This is in striking contrast to pH 3.2, where the number of perithecia per plate generally exceeded 500 (Plate IV).

Regarding the effect of pH on vegetative growth and perithecial development, the following conclusions may be drawn: (a) Two different pH optima exist with respect to these two functions. (b) The optimum pH for perithecial development seems to be regulated by factors governing sub-optimal vegetative growth. (c) pH optima for both functions are consistently higher in the case of *G. vulgaris*.

Effect of malt extract (Expt. 3).

An attempt has been made to determine the effect of malt extract in various concentrations, using Leonian's agar as the basic medium. Previous efforts to cultivate *Gnomonia* on media lacking malt extract were unsuccessful, nor does the fungus grow on a medium containing malt extract as its sole constituent.

Three series were set up: (a) Using Leonian's original formula. (Discussed previously under Expt. 1.) (b) The same, but with double the original quantity of malt extract. (c) The same, but with five times the amount of malt extract recommended by Leonian.

The plates were inoculated with *G. intermedia*.

Series (b) and (c) were started simultaneously with (a), under the same conditions of temperature and pH, viz., 19° C and pH 5.6 (after autoclaving).

It was decided to use the higher pH value of 5.6 at which both vegetative growth and perithecial development are relatively good, rather than the lower pH value of 3.2 which favours perithecial development alone. Colonies were measured in the usual manner, and the degree of perithecial development by counting the number of perithecia per plate. Results are illustrated in Fig. 4, curves I' and II', and in Table I.

The effect of doubling the amount of malt extract is a corresponding increase in the relative growth rate. The temperature-growth optimum remains the same, as does the temperature optimum for perithecial development. Similarly, perithecial development is strongly stimulated, while its temperature optimum seems to be unchanged.

Attempts to measure the (c) cultures were unsuccessful due to the irregular way in which the colonies developed. There was a strikingly profuse mycelial development, the aerial mycelium spreading over the sides and even the lids of the petri dishes. Perithecial development was entirely depressed.

It seems clear from this experiment that a slight increase in the amount of malt extract is stimulative both to vegetative growth and to perithecial development. Higher concentrations, while causing a marked stimulation in the former, have the effect of completely depressing the latter.

Institute of Physiological Botany, University of Uppsala, November 7 1951.

Summary.

(1) *Gnomonia vulgaris* Ces. et de Not. and *Gnomonia intermedia* Rehm on *Corylus avellana* and *Betula pubescens* respectively, have been isolated in pure culture.

(2) The growth-temperature range of *G. intermedia* is greater than that of *G. vulgaris*. The optimum growth-temperature for *G. vulgaris* appears to be about 17° C, that of *G. intermedia* about 19° C. In *G. intermedia*, perithecial development occurs at temperatures ranging from about 5° C to 19° C. *G. vulgaris* forms perithecia within a relatively narrow temperature range, viz., about 10° C to 19° C.

(3) *G. vulgaris* has an optimum growth-pH of 5.7, while that of *G. intermedia* lies around 4.3. The latter appears to be more tolerant of an extremely acid medium. The greatest number of perithecia occurred at pH 5.2 in the case of *G. vulgaris*, at pH 3.2 in that of *G. intermedia*.

(4) A slight increase in the amount of malt extract in Leonian's medium stimulates both vegetative growth and perithecial development of *G. intermedia*. Higher concentrations have the effect of completely depressing the latter function.

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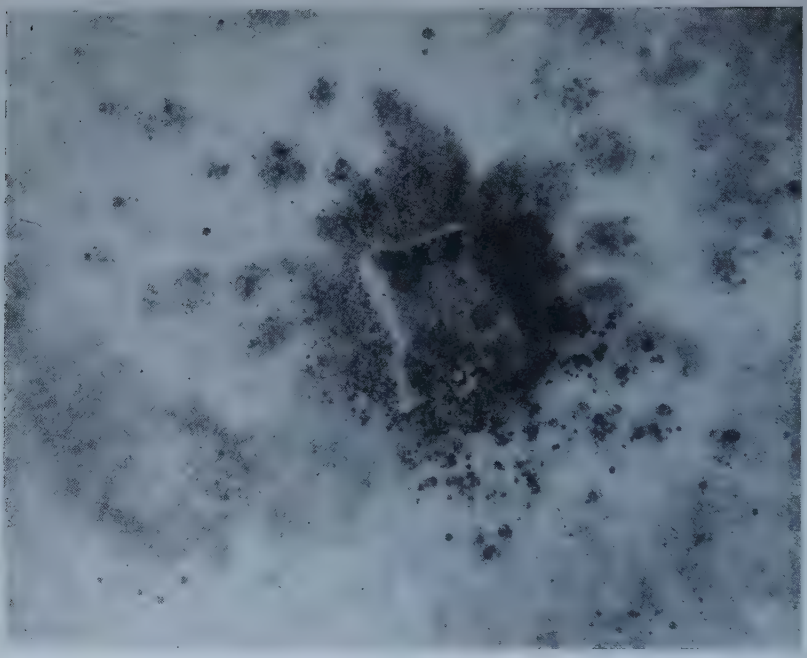
A

B



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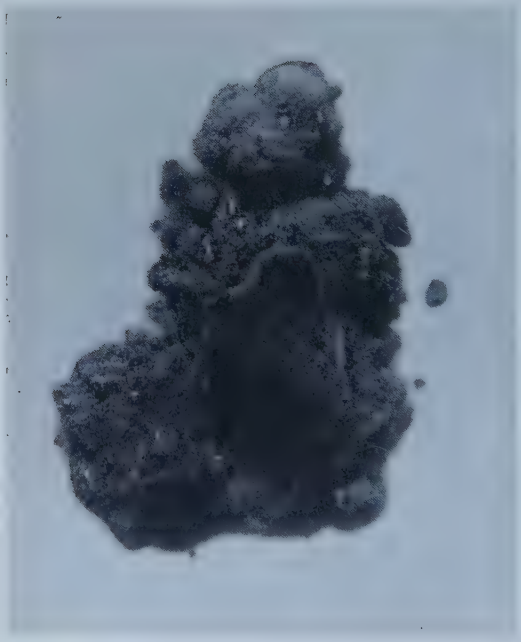

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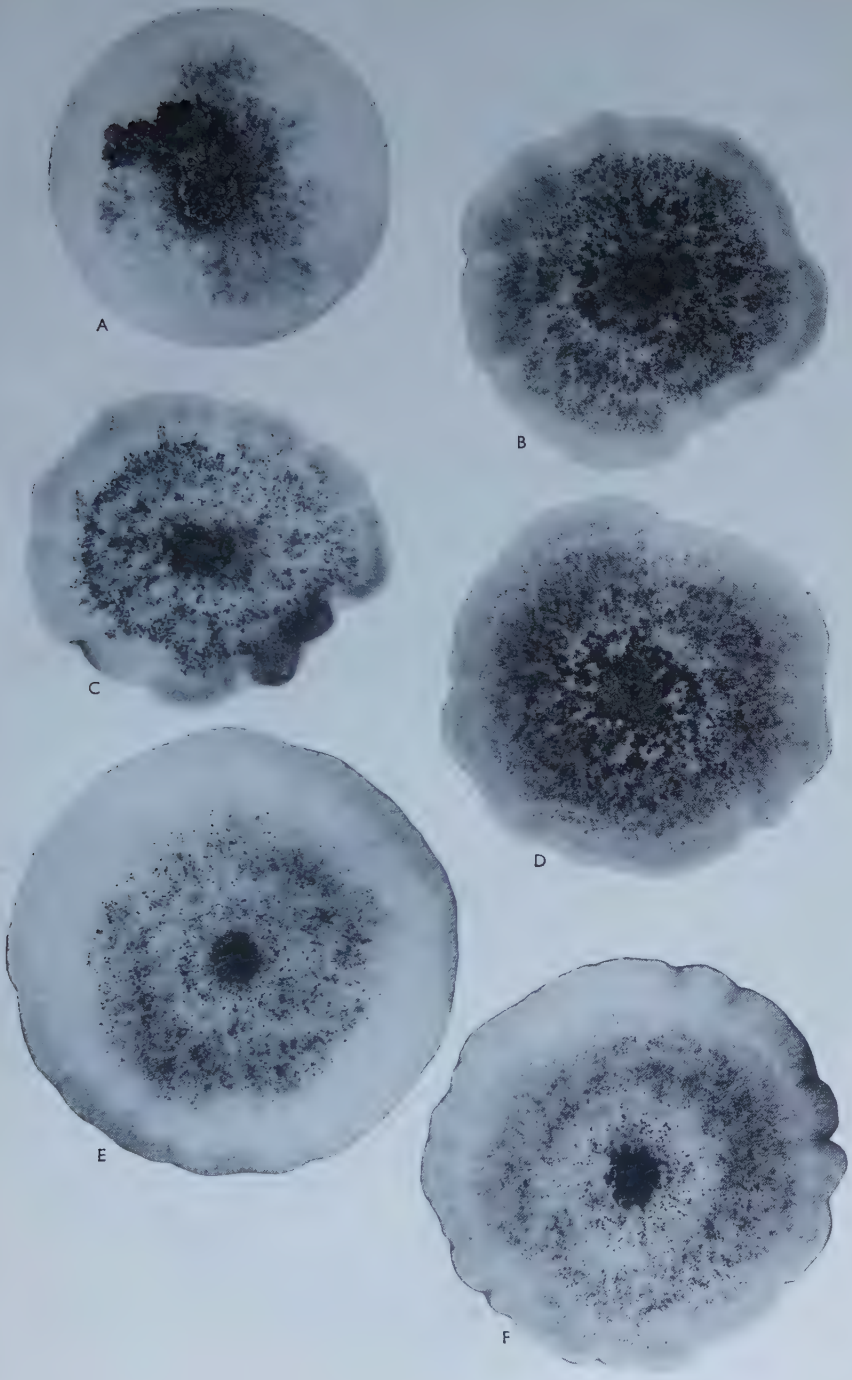
A
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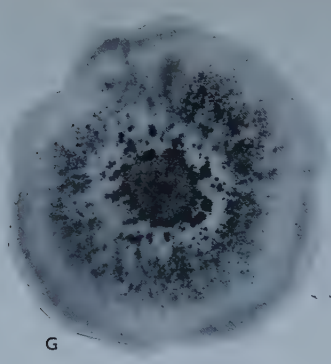

G

H

G. 1.

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Plate I and II.

Gnomonia vulgaris. Effect of temperature on perithecial development. A = 10° C; B = 15° C; C = 19° C; D = 25° C; E = 30° C. Cultures 25 days old. (5 × natural size)

Plate III.

Gnomonia vulgaris. Effect of pH on perithecial development. A = pH 3.2; B = pH 4.3; C = pH 4.8; D = pH 5.2; E = pH 5.4: F = pH 5.7. (Natural size).

Plate IV.

Gnomonia vulgaris (continuation of Plate III). G = pH 6.6; H = pH 7.1. Cultures 25 days old. (Natural size).

Gnomonia intermedia (= G. I.). Effect of pH on perithecial development. pH = 3.2. Culture 36 days old. (About natural size).

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ON THE FOSSIL CHAROPHYTA OF LATIN AMERICA.

BY

HENNING HORN AF RANTZIEN.

The recent distribution of the Charophyta in Latin America presents some intricate problems which are impossible to interprete without consideration to their past history in this region. Knowledge of the fossil forms is thus necessary. Fossil Latin American charophytes have been recorded from Hispaniola, Venezuela, Brazil, Argentina, and Peru; they range from the Lower Cretaceous to late Pleistocene. A survey of the finds is presented below. The present material is too scarce to permit the drawing of other than taxonomical conclusions. Further investigations are greatly hampered by lack of adequate material. Fossil charophytes are mostly found in marl deposits which are generally poor in other plant remains. For that reason these beds are often neglected by collectors. Without doubt, the fossil charophytes recorded from this region only represent an insignificant part of the material which can be gained by further collecting in the field.

An intensified search for fossil charophytes in the Latin American countries may be important also from other points of view. Studies of a corresponding material from other regions bear witness of the significant results which may be obtained in this field of research. The notable discoveries of the last 15 years by Th. M. Harris in Britain, by R. E. Peck and collaborators in the Rocky Mountain region of the United States, and by K. S. Rao and S. R. N. Rao in India, have contributed much to our present understanding of this group of plants.

The present investigation has been accomplished under the supervision of professor O. H. Selling, Director of the Paleobotanical

Department of the Riksmuseum. The writer is greatly indebted to him for much help with the literature, for profitable discussions on various aspects of the subject, and for facilities put at my disposal. Without his help and encouragement, this study would not have been carried through.

The Preservation of Fossil Charophyta.

Some introductory notes on the preservation of Charophyta as fossils and on the ecological basis of this preservation may be suitable; misunderstandings on this point are sometimes met with in the literature. A comparison with the biology and morphology of recent forms may elucidate this point.

In the fossil state, Charophyta are represented by oogonia and oospores, antheridia, stems, and other vegetative parts. Oospores and oogonia are the most common remains encountered (Groves & Bullock-Webster 1924, Pia 1927, Groves 1933, Peck 1946). Stems and other vegetative matter have been found occasionally; they are generally badly fragmented. Jurassic and Eocene forms have been found with the vegetative parts fairly well preserved (*Clavator* Reid & Groves 1916, *Perimneste* Harris 1939, *Lagynophora* Stache 1880). Calcified antheridia have been recorded from the Purbeck Beds of England (Harris 1939, p. 54); similar remains have recently been found in the Lower Cretaceous of Idaho, Wyoming, and Texas (Peck 1941, p. 295).

Apart from the comparatively few records of silicified charophytes (*e. g.* Peck 1934, p. 98), fossil remains of this group are calcified. Female reproductive bodies of fossil charophytes are believed to be preserved by virtue of their ability to secrete calcium carbonate from the spiral cells (Groves 1933, p. 3; Peck 1934, p. 89; 1946, p. 275). The deposition starts from the concave inner walls of the enveloping cells and may finally replace the cell contents. In late stages the lateral cell walls may break down and a kind of lime-shell thus envelop the interior. A corresponding incrustation may be seen in stem and branchlets. In recent charophytes, the antheridia and the coronula cells of the oogonia do not calcify. According to Peck (1941, p. 290; 1946, p. 275) calcified coronula cells have been preserved in *Aclistochara;* the nature of these structures is, however, disputed (cf. *e. g.* Rao & Rao 1939, p. 2; Peck & Reker 1947, p. 5). The physiological basis of this secretion is not fully understood.

Table I. Size of oogonia an

Species	Sample	Origin
Nitella flexilis Ag.	100 oog. + 100 oosp.	Sweden, Södermanland, Lake Bysjön
Tolypella prolifera v. Leonh.	General figure	Britain
Lychnothamnus barbatus (Meyen) v. Leonh.	General figure	Central Europe
Lamprothamnium papulosum Groves	General figure	Britain
Chara evoluta T. F. Allen	General figure	centr. and west. North Amer.
Chara corallina Willd.	General figure	tropical Asia
Chara hydropitys Reichb. v. *majuscula* Nordst.	100 oog. + 100 oosp.	Surinam

Similar secretions in aquatic plants have been discussed by Arens (1936, 1938, and for *Nitella*, 1946).

The calcification takes place in living cells only. When the anterior walls of the enveloping cells of an oogonium dissolve at maturity, the secretion of calcium carbonate ceases. Characteristic for the secretion is furthermore that it may begin at various stages of maturity of the oogonia. This may be due to external conditions. If calcification begins at an early stage, the enveloping cells will be filled with the secrete and the lime-shell will show the structural characters of the charophyte oogonium, *viz.* broad spiral convolutions separated by narrow furrows. If, on the other side, calcification begins later, only a thin layer of lime will be formed in the enveloping cells before the anterior walls dissolve. Accordingly, the specimen will show the structural pecularities of an oospore: sharp spiral ridges (*i. e.* the lateral cell walls) separated by wide concavities. Transitions occur; nevertheless, the extremes seem to merit distinction in descriptions of fossil specimens.

Both structures are generally classified as oogonia in the literature of fossil Charophyta. This may be right (for critical con-

oospores in some recent Charophyta.

Reference	Oogonia		Oospores	
	Pol. axis, μ extremes and mean	Equat. diam., μ extremes and mean	Pol. axis, μ extremes and mean	Equat. diam., μ extremes and mean
orig.	616 678 748	594 619 660	506 562 594	418 453 484
Groves & Bullock-Webster 1920, p. 134; recalculated	450 — 510	400 — 450	330 — 400	250 — 330
Migula 1897, p. 294	1 100 — 1 300	700 — 800	660 — 720	460 — 500
Groves & Bullock-Webster 1924, p. 8	750 — 950	400 — 575	600 — 750	275 — 375
Robinson 1906, p. 262; recalculated	620 — 780	400 — 500	580 — 680	330 — 370
Zaneveld, 1940, p. 133	925 — 1 230	600 — 900	645 — 875	525 — 605
orig.	550 583 616	352 391 440	396 440 506	242 286 330

siderations on this term, see *e. g.* Smith 1938, p. 131; Wood 1947, p. 241). In most studies of recent Charophyta, the term oogonium is used for the whole female structure (oosphere, coronula cells and enveloping cells); the latter are visible as broad spiral convolutions. The zygote, the oospore, is of a corresponding composition but is structurally characterized by the displaying of sharp spiral ridges. The enveloping cells are represented only by the concavities between the ridges. The same terminology is adopted in the present paper. It is to be noted however, that a considerable part of the fossil "oogonia" with broad spiral convolutions may be oospores where the enveloping cells have been filled with lime before the dissolution of the walls; to their outer morphology, they correspond entirely to oogonia as defined here. The lateral sutures should not be interpreted as accidentally preserved parts of the enveloping cells. It is important to emphasize that the lateral and posterior walls of the enveloping cells change chemically during post-fertilization; the result is a tough and strongly coloured sheltering membrane, containing suberin and silicic acid (Nordstedt 1889, p. 3); this is an organic part of the oospore, forming its

outermost layer, as has been proved by GROVES & BULLOCK-WEBSTER (1920, p. 57).

This may not only be a matter of terminology. In modern forms, cogonia and oospores always differ in size *inter se*: a complete mature cogonium is larger than the oospore to which it gives rise. This tendency in recent material is illustrated in Tab. I. It is to be noted that the figures in the Tab. are not directly comparable, as they have been calculated or recalculated from samples of very different sizes. The height of the coronula is excluded from all measurements.

Historical Review.

In view of their value as stratigraphic fossils, Cretaceous and Tertiary charophytes have been studied intensely in Central Europe, Britain, western United States, and India. The fossil charophyte flora of Latin America has been much neglected. An intensified search for these fossils, especially in the Cordillera region, would certainly reveal abundant material and interesting results.

A fossil charophyte from this area was recorded already by ETHERIDGE (1879, p. 82; cf. OLIVEIRA ROXO 1924, p. 51) from the Tertiary of Solimões, Brazil. The specimens were not described, and cannot be identified. The first fossil plant of this group specifically identified from Latin America was *Chara woodringii* E. W. BERRY from the Miocene of Haiti, Hispaniola (E. W. BERRY 1922, p. 3). Two species of *Chara* have been described from Cretaceous beds at Jujuy, northern Argentine (FRITZSCHE 1924, p. 28). The fossil charophytes described up to 1933 were summarized by GROVES (1933). A remarkable Pleistocene find from northern Venezuela was reported by CH. T. BERRY (1934, p. 390). PECK & REKER (1947, pp. 3—5) recorded four species of *Chara* and a member of the allied genus *Aclistochara* from the Cretaceous and early Tertiary of Peru. Recently, some Upper Cretaceous or Lower Tertiary charophyte remains from Peru according to determination by PECK were tentatively referred to *Ac[lis]tochara mitella* PECK & REKER (JENKS 1951, p. 214).

Review of the Species.

Recent important discoveries, especially in the Devonian and the Lower Cretaceous of the Rocky Mountain region and the Purbeck

of England, have made the classifications of fossil Charophyta by Pia (1927) and Groves (1933) somewhat outdated. In Peck's very brief outline (1946) four families are recognized: *Characeae*, *Clavatoraceae*, *Trochilischaceae*, and *Sycidiaceae*. Up to now, only the first-mentioned family has been found in the area discussed in this paper.

The two genera of *Characeae* reported from Latin America are distict in the following characters (Peck 1937, p. 86; 1941, p. 290; Peck & Reker 1947, p. 5):

Enveloping cells ascend to the junction area of apical pole without apparent change in size or shape ..... *Chara*

Enveloping cells abruptly narrowed in periphery of apical pole, then turning abruptly into center of pole, strongly expanding in width ..... *Aclistochara*

Family Characeae.

Genus Chara L.

Chara L., Sp. Pl. (1753) p. 1156.

Generic type: *Chara tomentosa* L., l. c. (cf. Horn af Rantzien & Olsen 1949, p. 99).

Undisputed coronula cells have not been found in fossil charophytes. The major classification of the recent Characeae into two tribes (or other suprageneric categories) is based on characters relating to the structure of the coronula. For that reason it is often very difficult to refer fossil specimens to any of these groups with certainty. Pia (1927, p. 89) solved the problem by referring all fossil oogonia (and oospores) to the form genus *Gyrogonites* Lam. This method has not been generally adopted (cf. Groves 1933, p. 11; Peck 1941, pp. 288—289). Groves (l. c.) emphasized that *Gyrogonites* might be revived, but the genus should be confined to only such remains as obviously do not belong to *Chara* (*e. g. C. medicaginula* Brongn.). Of the numerous Cretaceous and Tertiary species of *Chara* described, a fairly large part belong to this genus with every probability. — *Gyrogonites* has been reintroduced by Harris (1939, p. 12) in the form »gyrogonite» as a designation of the inner part of the oogonium in fossil Charophyta. This term appears very suitable.

Chara monilifera Peck & Reker.

Chara monilifera Peck & Reker, Amer. Mus. Novit., 1369 (1947) p. 4, figs. 12—18.

"Oogonia small, spherical, ranging from 0.42 to 0.52 mm. in length and width. Spiral ridges low, intercellular in position, and partially obscured by prominent, regularly arranged tubercles. Seven or eight spirals visible in lateral view. Base on most specimens marked by small, centrally placed node, summit area by five tubercles arranged in a circle or ellipse" (Peck & Reker l. c.).

Eocene, possibly Oligocene, 16.5 km "N. 57 E." of Contamana Cemetery, Loreto, Peru (Am. Mus. Nat. Hist. 26408: 1 — holotype).

Description and figures appear to be based on oogonia and oospores (figs. 16—17: typical oogonia; fig. 12: oospore). The type material contains about 100 specimens, all rather uniform in size and shape.

C. monilifera is distinguished by small size, spherical shape, and extensive development of tubercles. Species of *Chara* with tuberculate oogonia and oospores are restricted to the Eocene and Oligocene (as to the Jurassic *C. bleicheri* Sap., see Peck & Reker 1947, p. 4; 1948, p. 85) but apparently had a world-wide distribution. The presence of tubercles and their systematic significance, is discussed by Peck & Reker (1948, p. 88):

"Tubercles may have little if any systematic value in the classification of the charophytes . . . . . It is not unlikely that a tendency to develop tubercles is restricted to certain species and that environment controls the expression of the inherent tendency. Stage of growth may also be a factor in their development . . . . ."

It has been proved that the tubercles contain organic substance (Reid & Groves 1921, p. 185); they are consequently not the result of accumulation of calcium carbonate, and are assumed to have been present in the living plants. In certain early Tertiary species, tubercles or traces of them have never been observed; they apparently had no tendency to form structures of this kind. In other species, tubercles are found in various stages of development or they may be absent in some specimens. It seems likely that different stages of growth are responsible for this variation, in the same way as *e. g.* the delicate sculpture of the oospore membranes in recent species is scarcely or not at all visible in young oospores but becomes strongly developed and characteristic at approaching maturity. Environment is not known to cause effects of this kind in the oospores of recent species. The tendency to form tubercles, which is entirely unknown in recent species, appears to the writer as of certain systematic importance. It is of course not quite reliable at the specific identification of a very small specimen sample, however.

Chara ovalis Fritzsche.

Chara (*Nitella*?) *ovalis* Fritzsche, Neues Jahrb. f. Min., Geol. u. Pal., 50, Beil. Bd (1924) p. 28, pl. II, fig. 2.

Chara ovalis Groves in Jongmans, Foss. Cat., 19 (1933) p. 27; Peck & Reker, Amer. Mus. Novit., 1369 (1947) p. 3, figs. 7—11.

"Oogonien längs-oval mit 9—10 glatten, mässig schräg verlaufenden Rindenzellsegmenten auf der hemisphärischen Seitenfläche. Die Aussenwände sind convex und durch vertiefte Nahtlinien geschieden. Ein Krönchen ist nicht vorhanden, so dass die Zurechnung der Spezies zu *Chara* unsicher bleiben muss, zumal auch die Zahl der Rindenzellsegmente keinen festen Anhalt gibt" (Fritzsche l. c.).

"Oogonia ellipsoid to ovoid with greatest diameter at or below the middle, size variable, ranging from 0.70 mm. to 1.30 mm. in length and 0.63 mm. to 1.04 mm. in width. Spiral ridges prominent, intercellular in position, eight or nine (rarely seven or 10) visible in lateral view. Spirals fail to join at summit, leaving small opening into oogonium, base round" (Peck & Reker l. c.).

Cretaceous, between Tres Cruces and Negra Muerta, Jujuy, Argentine (holotype, location unknown). — Cretaceous, Huayllabamba formation, 2.5 km NE of Cuzco, Peru; Cretaceous, Vilquechico formation, 1 km SE of Vilquechico, Puno, Peru; same formation, 4 km ESE of Putina, Puno, Peru; Cretaceous, Moho group, 4 km SE of Moho, Puno, Peru.

Fritzsche's drawing shows an oogonium with maximum equatorial diam. at the middle, a rounded apical pole, a slightly protruding base, and with the enveloping cells exhibiting nine convolutions. According to the scale of magnification the polar axis appears to be about 760 μ, the equatorial width about 600 μ.

The description by Peck & Reker (l. c.) is stated to be based upon more than 100 specimens designated as oogonia. An oospore is reproduced in figs. 9—10.

This species was referred to either of the genera *Chara* or *Nitella* by Fritzsche (l. c.). There is, however, no reason to suppose that it should belong to the latter genus.

Peck & Reker were not able to spot the type when identifying the abundant Peru material. The authors state: "The illustration of *C. ovalis* given by Fritzsche is a generalized drawing to which many species of oogonia might be referred. Although the specific identity of the Peru form is therefore uncertain, we can see no satisfactory means by which they may be differentiated without further knowledge of the type." Considering the large and confluent variation in the numerous specimens referred by Peck & Reker to

C. ovalis, the type as described and figured by FRITZSCHE must be said to fit fairly well within the limits of this variation. The specific identity assumed by PECK & REKER thus seems very probable.

Chara perlata Peck & Reker.

Chara perlata PECK & REKER, Amer. Mus. Novit., 1369 (1947) p. 3, figs. 19—21.

"Oogonia almost spherical, slightly broader than long, length 0.78 mm. and width 0.81 mm. with only slight variations in dimensions. Spiral ridges intercellular in position, seven or eight visible in a lateral view. Summit and basal areas broadly rounded to almost flat" (PECK & REKER l. c.).

Cretaceous, Vilquechico formation, 1 km SE of Vilquechico, Puno, Peru; same formation, 4 km ESE of Putina, Puno, Peru. — Locality of holotype not given; the holotype is Am. Mus. Nat. Hist. 26407: 1.

C. perlata is fairly distinct in that its equatorial width is greater than its polar length. Similar Tertiary forms have been recorded (*C. compressa* KNOWLTON 1888, p. 156, recently transferred to *Aclistochara* by PECK & REKER 1948, p. 87; *C. oehlerti* DOLLFUS 1921, p. 88; *C. rajahmundrica* RAO & RAO 1939, p. 9); they are considerably larger, however.

In the Peru localities, *C. perlata* is found together with *C. ovalis*. It is undoubtedly distinct from the latter.

Chara sejuncta Braun.

Chara sejuncta BRAUN, Boston Jour. Nat. Hist., 5 (1845) p. 264, footnote.
Chara requena CH. T. BERRY, Jour. Wash. Acad. Sci., 24 (1934) p. 390, figs. 6—7.

For synonymy of the recent species, see HORN AF RANTZIEN 1950, p. 397.

"The oogonium is very minute, being 79.8 μ long and 52.5 μ broad. It is elliptical in profile and circular in cross section. There are 12 convolutions which form a low spiral. The spiral cells are concave making a deep furrow between the extended keels of the cell margins. The width of the cell taken from keel to keel is 5.8 μ in the center region of the oogonium. There is a round hole at the basal end while the cells unite in a low nondescript rosette at the apical end" (CH. T. BERRY l. c.).

Pleistocene, at the eastern end of Lake Tacarigua (=L. Maracay), northern Venezuela. — *C. sejuncta* ranges from Massachusetts and Minnesota through Alabama, Mexico, and the West Indies to Colombia, Bolivia, and Brazil (ROBINSON 1906, p. 297; HORN AF RANTZIEN 1950. p. 398). The type is Brazilian.

C. requena is stated to have been described from six oogonia. The description is accompanied by two excellent drawings. Fig. 6 represents an oospore with 12 ridges, well agreeing with the "oogonia' described, though according to the scale of magnification the polar axis is c. 800 μ, and the equatorial diameter c. 525 μ. Fig. 7 illustrates a picee of stem with two nodes, the upper apparently bearing six branchlets, the lower seven. No details of stipulodes or cortex can be observed. The stem appears to have a diameter of c. 0.5 mm.

There are controversial statements as to the size of the specimen. The length of the polar axis varies greatly among charophyte oospores. The limit values are c. 150 μ (it is doubtful however, whether so low values refer to quite mature specimens) and c. 1400 μ. Values below 350 μ or above 850 μ are not very common. In fossil species, large values are more frequent. The smallest oogonium of any Tertiary charophyte known (*C. perpusilla* Groves 1926, p. 173) has the polar axis 275—300 μ long. In certain recent species of *Nitella*, mature oospores range from 200 to 250 μ in length. A stated oospore length of 79.8 μ for the apparently late Pleistocene *C. requena* would thus be unique for this species, and is rather unlikely. — A still stronger and fairly conclusive argument against the size stated in Berry's description is the width of the enveloping cells. There is some relation between the length of an oogonium or oospore and the number of convolutions or ridges seen in lateral view. Though exceptions do occur, small oogonia tend to have fewer convolutions than large ones. The average diameter of the enveloping cells is generally between 40 and 70 μ. A "width of the cell taken from keel to keel" of 5.8 μ (Berry's description) is not very likely, whilst a diameter of c. 60 μ would seem to be normal. For the reasons given above, the information as to size that can be derived from Berry's figure is considered correct; corresponding statements in the description may be due to an error of calculation.

The Pleistocene deposit including *C. requena* is comparatively recent. It was found in a bed of calcareous marl, containing remains of fish, molluscs, crustaceans, diatoms, and sponge spicules, the species composition indicating that the marl had been deposited in a fresh-water lake with clear water. Immediately above this bed, piles of wood were found, upon which a lake-dwelling tribe had built their huts. The whole was covered by about 3 m of top soil. Exact age of bed is unknown.

With respect to the late origin of the matrix, it appeared from the first probable that *C. requena* is still extant in the region. The size and circular cross section of the oospore and the structure of the stem as figured by BERRY make it definitely clear that the specimens are to be referred to *Chara s. str.* Among the recent species occurring in Latin America *C. requena* corresponds very closely to *C. sejuncta* BRAUN. For reasons given below, the writer considers the identity of *C. requena* with that species fairly safely based.

An oospore length of 750—800 μ is reached by only five recent species of *Chara* occurring in Latin America: *C. aculeolata* KÜTZ., *C. braunii* GMEL., *C. hornemannii* WALLM., *C. sejuncta* BRAUN, and *C. zeylanica* WILLD. In order to spare some space abbreviations will be used for the species discussed, *viz.*, *ac*, *br*, *ho*, *se*, *zey*, and *req*. The largest dimensions recorded in the literature for oospores of these species are (polar axis × equat. diam.; dimensions in μ): *ac* 800×600, *br* 750×575, *ho* 800×480, *se* 910×660, *zey* 750×540. It is to be noted that these maximum values are rarely observed, the bulk of specimens is much smaller. If a single or few oospores are collected at random, there is consequently only a rather small chance that it or they should attain the dimensions given. It is furthermore of some interest that the relation $\frac{\text{polar axis}}{\text{equat. diam.}}$ is rather constant in *br* and *se*, more fluctuating in *ac*, *ho*, and *zey*. The number of ridges displayed by the oospores are *ac* 13—14, *br* 7—12, *ho* 5—12, *se* 12—15, *zey* 10—15. BERRY's fig. of the piece of stem of *req* shows clearly that this plant was heavily incrusted; also *ac*, *ho*, *se*, and *zey* are more of less often incrusted, *br*, on the contrary, is not at all or only slightly incrusted. With regard to the present distribution, *ac* is restricted in Latin America to the Cordilleran region from Bolivia to southern Chile with increasing frequency southwards; the other four species are more or less frequent in northern South America, the West Indies, etc. The data derived from this comparison can be summarized thus:

1. *ac* attains an extreme length of the polar axis of c. 800 μ; such very large specimens tend to be relatively broader than in *req*; a Boreal and Andine species not observed in the region.

2. extreme length of *br* is only c. 750 μ; oospores relatively much broader; common in the region; not at all or slightly incrusted.

3. *ho* attains an extreme length of the polar axis of c. 800 μ; such very large oospores are more elongate than those of *req*; common in the region.

4. oospores of *se* reach a maximum length of c. 910 μ, the minimum length is about 660 μ, the length of c. 800 μ as given for *req.* is not unfrequent in *se*; the length/width relation is apparently rather similar to that of *req*; common in the region.

5. extreme length of *zey* is only c. 750; oospores relatively much broader; common in the region.

It appears that *br* and *zey* may be excluded at once because of their broad and more rounded oospores; oospores of *ac* and *ho* do reach a length of c. 800 μ, though this represents rare maximum dimensions, *ac* is also very unlikely because of phytogeographical reasons, *ho* not very likely on account of the more elongate oospores. *C. sejuncta* is accordingly the only Latin American species closely corresponding to *C. requena* in oospore characters. No structures telling against an affinity with that species have been observed in the fossil plant.

Chara strobilicarpa Reid & Groves.

Chara strobilicarpa Reid & Groves, Quart. Jour. Geol. Soc. London, 77 (1921) p. 187, pl. 5, figs. 7—8; Groves in Jongmans, Foss. Cat., 19 (1933) p. 31; (?) Rao & Rao, Mem. Geol. Surv. India, 29:2 (1939) p. 7, pl. 1, fig. 7, pl. 2, fig. 7; Peck & Reker, Amer. Mus. Novit., 1369 (1947) p. 4, figs. 1—6.

Gyrogonites strobilicarpus Pia in Hirmer, Paläobotanik I (1927) p. 90.

"Oogonium obovoideum deorsum conspicue fastigatum, apice rotundato, long. 850—1000 μ, crass. 550 –600 μ; cellulae spirales concavae, lat. c. 100—125 μ, ad apicem et basem dilatae, convolutiones novemundecim exhibentes; foramen basilare parvum, valde angulatum" (Reid & Groves l. c.).

Upper Eocene, Lower Headon Beds, Hordle, Hampshire, England (holotype). — Eocene, possibly Oligocene, 16.5 km "N. 57 E." of Contamana Cemetery, Loreto, Peru. — Also recorded by Rao & Rao (l. c.) for the Deccan Inter-trappeans near Rajahmundry, India.

The description by Peck & Reker (l. c.) agrees well with the diagnosis of the type material. The authors figure oogonia (figs. 1, 3, 6, possibly 2, 5) and one oospore (fig. 4). The specimens illustrated show considerable variation as to size and shape. Two forms are represented, a large obovoid type (fig. 1), and a smaller, slender, elongate type (fig. 6). The two extremes intergrade.

Comparison of shape and degree of maturity in oogonia of recent species shows that the strong variation in the Peru material as described and figured by Peck & Reker is probably due to stage of growth. A young oogonium is characterized by an elongate form; when approaching maturity, its equatorial diameter tends to increase more than its polar axis. It is therefore suggested that the small, slender and elongate specimens are immature oogonia. On this assumption the broad, obovoid type of oogonium (figs. 1 and 3) may be considered typical of *C. strobilicarpa*.

This is a distinct and fairly characteristic species. Distinguishing characters are in the first place its considerable size, the sharp taper

towards the base, the rounded apical pole, and the arrangement of the tips of the enveloping cells. On account of their circular cross section and size, these specimens are likely to represent a true *Chara*. Of the fossil charophytes from this area, it is the only one recorded with certainty from the Old World.

Chara woodringii E. W. Berry.

Chara woodringii E. W. Berry, Proc. U. S. Nat. Mus., 62: 14 (1922) p. 3, fig. 1; Groves in Jongmans, Foss. Cat., 19 (1933) p. 36.
Gyrogonites woodringii Pia in Hirmer, Paläobotanik I (1927) p. 90.

»Oogonium circular in cross section; elliptical in profile, slightly fuller distad than proximad; somewhat variable in size, which ranges from 0.5 to 0.8 millimeter in diameter, and from 0.75 to 1.25 millimeters in length. Proximal pole with a thin pentagonal calcareous plug which is frequently broken away. Apical pole consisting of the tips of the five cells which are enlarged and slightly thickened. The five cells of the wall make three revolutions, the spirals are hence low, and are roundly furrowed between the knife-edge extended keels of the cell margins" (E. W. Berry l. c.).

Miocene, Haiti, "W 96 F (U. S. G. S. fossil plant station 7555). Dép. du Sud, Vallée de l'Asile, south side of Rivière Serpent between Source Paul and Source Goudet. W. P. Woodring, collector. November 16, 1920" (Berry op. c. p. 2).

The description is supplemented by four somewhat schematical drawings: a. probable oospore, apical view; b. oospore, lateral view; c. cross section of space between two adjacent oospore ridges; d. probable oospore, basal view. The drawings agree well with the description, except that in fig. 1 b the oospore in lateral view is figured as strongly tapering towards both poles; it is provided with 15 or 16 ridges. The magnification is not stated.

From the description and the figures it can be clearly seen that the type material is entirely or to the major part represented by oospores. The circular cross section and large size bear witness of that *C. woodringii* probably is a *Chara s. str.*

The generalized drawings make it difficult to compare *C. woodringii* with the other charophytes reported from this area. As described and figured by Berry, it can scarcely be identified with any recent or fossil species recorded from Latin America. Apparently it also stands apart from the numerous fossil Charas reported from the United States. Principal distinguishing characters of the oospore are: its size, large number of ridges, and peculiar elliptic

shape. Judging by the figure by UNGER (1852, pl. 25, fig. 10; cf. ETTINGSHAUSEN 1872, p. 162), the Oligocene Yugoslavian *C. ungeri* ETT. may be of similar appearance.

Chara sp.

Chara sp. ETHERIDGE, Quart. Jour. Geol. Soc., 35 (1879) p. 82. — *Chara* sp. OLIVEIRA ROXO, Serv. Geol. Min. do Brazil, 11: Contr. Paleont. Valle Amaz. (1924) p. 51.

Tertiary, Canama, Rio Javary, Solimões, Brazil.

The specimens recorded from this locality were not described, and cannot be identified. OLIVEIRA ROXO (l. c.) only mentions the find with reference to ETHERIDGE's paper.

Genus Aclistochara (PECK) PECK.

Aclistochara PECK, Jour. Paleont., 11 (1937) p. 86; PECK, ibid., 15 (1941) p. 290, emend.

Generic type: *Aclistochara bransonii* PECK, Jour. Paleont., 11 (1937) p. 87.

The genus *Aclistochara* was first defined as having a truncate summit and enveloping cells leaving a conspicuous opening at the apical pole into the interior of the oogonium, this in contradistinction to *Chara*, where the tips of the enveloping cells join immediately below the coronula cells without any large hole (PECK 1937, p. 86). A study of further specimens referred to *Aclistochara* revealed the presence of structures interpreted as coronula cells, or — if no such were present — indentations showing their former presence (PECK 1941, p. 290). Coronula cells of recent charophytes do not calcify, however (GROVES 1933, p. 3). The summit nodes observed in some fossil Charophyta have accordingly been considered terminal extensions of the enveloping cells (REID & GROVES 1921, p. 181; GROVES 1925, p. 12; 1926, p. 165; 1933, p. 3; RAO & RAO 1939, p. 2). Another opinion has been held by DOLLFUS & FRITEL (1919, p. 247), and PECK (1937, p. 87; 1941, p. 290; 1946, p. 277) who interprete these structures as true coronula cells. PECK & REKER (1947, p. 5) consider these collar-like extensions neither real coronula cells separated by a wall from the enveloping cells, nor simple terminal expansions, but organs *sui generis* of diagnostic value for this genus.

Specimens of *Aclistochara* are abundant in early Tertiary deposits of India, Italy, France, England, Peru, Florida, and the Rocky

Mountain region (Peck 1941, p. 287); they are also reported from the Tertiary of other countries *e. g.* Hungary (Rásky 1941, p. 300). Species of *Aclistochara* have furthermore been found in the Upper and Lower Cretaceous of the northern Rocky Mountains (Peck 1941, p. 287). In South America, two species are known from Tertiary beds in Peru, and one from the Cretaceous of Argentina. Vegetative remains have not been found together with oogonia and ospores.

Aclistochara cruciana new name.

Aclistochara cruciana new name.

Chara elliptica Fritzsche, Neues Jahrb. f. Min., Geol. u. Pal., 50, Beil. Bd (1924) p. 28, pl. II, fig. 3; Groves in Jongmans, Foss. Cat., 19 (1933) p. 17.

Not *Chara elliptica* Hislop, Quart. Jour. Geol. Soc., 16 (1860) p. 135, *nomen nudum.*

"Sie ist von quer-ovaler, scheinbar zusammengedrückter Gestalt und schliesst gegen den Krönchenaufsatz stumpf ab. Die Aussenwände der 6 Rindenzellschläuche sind convex und durch mässig eingetiefte Nahtlinien voneinander getrennt. Bei einem der Exemplare ist das Krönchen erhalten. Es ist sehr niedrig und besteht, soweit sich feststellen lässt, aus einzelligen Rindenschlauchenden; jedenfalls deutet nichts auf die Zweizelligkeit derselben hin" (Fritzsche l. c.).

Cretaceous, between Tres Cruces and Negra Muerta, Jujuy, Argentina (holotype, location unknown).

The drawing represents an oogonium in summit view. Contrary to Fritzsche's description, the oogonium appears to be of circular cross section. The apical structure interpreted as a coronula is clearly visible. It apparently consists of the apical ends of the enveloping cells; these are contracted in the summit periphery, and turn up much expanded in the center. No dimensions are given in the description; judging by the magnification of the figure, the equatorial oogonium diameter appears to be c. 485 μ.

The statement in the description as to "6 Rindenzellschläuche" apparently refers to the number of convolutions displayed by the enveloping cells when seen in lateral view. The enveloping cells are invariably five in fossil and recent Characeae, except in the Upper Carboniferous *Palaeochara acadica* (Bell 1922, p. 160).

The apical pole of *C. elliptica* as described and figured by Fritzsche corresponds closely to the structures differentiating *Aclistochara* from *Chara s. str.* A "pseudo-coronula" of this kind has not been

observed in fossil specimens of the latter genus. Accordingly, it is suggested that *C. elliptica* Fritzsche should be transferred to the genus *Aclistochara*.

The scanty data derived from Fritzsche's description and figure make positive specific identification difficult. It seems certain, however, that the present plant cannot be identified with any of the Tertiary species listed below from Peru. *A. mitella* is characterized by larger oogonia with nine or ten spirals in lateral view. Also *A. supraplana* has much larger oogonia, well over 1 mm in equatorial width, provided with more convolutions. The Argentine plant also appears to differ from the numerous Tertiary Rocky Mountain species. Of special interest is comparison with two apparently very common species of *Aclistochara* from the Lower Cretaceous of Colorado, Utah, Idaho, and Wyoming (Peck 1941, pp. 290–292). Both species, *A. mundula* Peck and *A. cylindrica* Peck, appear from the descriptions and figures very unlike the Cretaceous species from Jujuy.

According to the present International Rules of Botanical Nomenclature (Art. 61), the name *C. elliptica* Fritzsche is nomenclaturally untenable, as there is an earlier — though illegitimate — homonym.

? Aclistochara mitella Peck & Reker.

Aclistochara mitella Peck & Reker, Jour. Paleont., 22 (1948) p. 89, pl. 21, figs. 16—20.

Actochara mitella Peck & Reker ex Jenks, Bull. Geol. Soc. Am., 62 (1951) p. 214. [Typographical error].

"Oogonia of medium size, 0.65 mm. to 0.73 mm. long, 0.52 mm. to 0.63 mm. wide, obovoid, with base normally projecting. Coronula cells present, but not conspicuous on some specimens. Nine or ten spirals visible in lateral view, with cellular ridges normally present" (Peck & Reker l. c.).

Lower Eocene, Evanston formation, Sublette County, Wyoming (Univ. Mo. 31025: 1 — holotype). — A charophyte closely resembling this species has been recorded from Lower Tertiary or late Upper Cretaceous, Calera quarry, Pocobamba formation, Cerro de Pasco, Peru.

Specimens from the Calera quarry were collected together with fresh water planorbids. The "charophyte oögonia" were forwarded to Peck, who stated that owing to their poor preservation they were not too diagnostic. "He would judge, however, that these charophytes are lower Tertiary or late Upper Cretaceous. They

closely resemble *Ac[lis]tochara mitella* Peck and Reker described from the Evanston formation of Wyoming" (Jenks l. c.).

Aclistochara supraplana Peck & Reker.

Aclistochara supraplana Peck & Reker, Amer. Mus. Novit., 1369 (1947) p. 5, figs 22—27.

"Oogonia large, broadly obovoid to almost spherical, 1.08 mm. to 1.35 mm. in length and 1.06 mm. to 1.31 mm. in width. Summit truncate, the spirals narrowing and becoming abruptly flattened at the summit periphery, then widening and remaining flat or becoming slightly swollen near the point of junction in the center of the summit, many specimens distinctly coronulate. Spirals on most specimens gently convex, on a few flattened or slightly concave, eight or nine (rarely seven or 10) visible in lateral view, no evidence of tubercles. Base strongly projecting on most specimens" (Peck & Reker l. c.).

Eocene, possibly Oligocene, 16. 5 km "N. 57 E." of Contamana Cemetery, Loreto, Peru (Am. Mus. Nat. Hist. 26410: 1 — holotype).

According to Peck & Reker (l. c.), this description is based on about 100 well preserved specimens. Both oogonia (figs. 23, 24, 27) and oospores (25, possibly 22 and 26) are figured.

A. supraplana is distinct by its large size, subspherical shape, and projecting base. It is apparently not closely allied to any other species of this genus, but shows points of resemblance to *Chara helicteres* Brongn. *s. str.* as described by Dollfus & Fritel (1919, p. 247).

Summary.

In connection with studies on recent Latin American Charophyta, the records of fossil charophytes from this area have been reviewed. Nine species are listed. Cretaceous are *Chara ovalis* Fritzsche em. Peck & Reker (Argentina, Peru), *C. perlata* Peck & Reker (Peru), and *Aclistochara cruciana* new name (= *C. elliptica* Fritzsche non Hislop; Argentina). *Chara monilifera* Peck & Reker (Peru), *C. strobilicarpa* Reid & Groves (Peru; Europe; ? India), and *Aclistochara supraplana* Peck & Reker (Peru) are Eocene or possibly Oligocene. *Chara woodringii* E. W. Berry (Haiti) is Miocene. Some specimens from the late Upper Cretaceous or Lower Tertiary of Peru are tentatively referred to *Aclistochara mitella* Peck & Reker. *Chara requena* Ch. T. Berry from late Pleistocene deposits in northern Venezuela is

here considered identical with the recent *C. sejuncta* BRAUN. An unidentified species of *Chara* has been reported from the Tertiary of Solimões, Brazil.

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SMÄRRE UPPSATSER OCH MEDDELANDEN.

Föreningens medlemmar uppmanas att till denna avdelning insända meddelanden om märkliga växtfynd o. d.

Phyllodoce coerulea (L.) Bab. i sydöstra Jämtland.

Karta 1370 i Hultén (1950) visar oss utbredningen för *Phyllodoce coerulea* i Norden. I sydöstra Jämtland står där ett frågetecken för växten. Genom en lycklig tillfällighet och tack vare värdefull hjälp av en av mina vänner i östra Jämtland, skogvaktaren Carl August Carlsson, Stavre, är jag i stånd att fastslå, att frågetecknet bör utbytas mot en prick. I samband med att C. A. Carlsson i våras meddelade mig ett par fyndorter för *Ledum palustre* i Revsunds socken skrev han, att socknen hyser åtskilliga växtlokaler, som ej äro upptagna i Lange (1938), såsom för *Myricaria germanica* och *Phyllodoce coerulea*. Å några berghällar hyser socknen *Viscaria alpina* (på östra sidan av Bodsjön vid Gimåns utlopp å två ställen, C. A. Carlsson, Stora Dyngdalen, C. A. Carlsson). Han inbjöd mig också till ett besök under sommaren för att ta växterna i skärskådande. Det var med hänsyn till uppgiften om *Phyllodoce coerulea* så pass lockande, att jag med glädje accepterade. Den 16 juni reste jag till Stavre på ett par dagar. Vi sågo *Ledum* å två lokaler, för vilka jag har för avsikt att senare närmare lämna en redogörelse i samband med ett meddelande om skvattram i landskapet. Vi besökte den rika *Myricaria*-lokalen i Revsunds socken på Ammerön vid Skurutjärn, vilken sjö sänkts för åtskilliga år tillbaka och där klådriset växer på en cirka 100 m lång sträcka och visar rik föryngring. Denna lokal ligger c:a 1 $^1/_2$—2 km väster om färjstället. Men allra intressantast var för mig att se *Phyllodoce coerulea* i socknen. Växtplatsen är en gles barrblandskog, rik på *Empetrum hermaphroditum*, cirka 300 m öster om Stavre by. Lappljungen växer här på två begränsade områden drygt 100 m från varandra. På det ena området finns *Phyllodoce* på en yta av omkr. 4 m². Då vi den 17 juni besökte lokalen, blommade ej lappljungen denna sena vår, ehuru den normala år brukar blomma här ett par veckor före midsommar. Men på många exemplar sågos blomknoppar. Minst 25 skott med blomställningar räknades. Detta område hyste utom en liten gran och en låg enbuske *Antennaria dioeca*, *Calluna vulgaris*, *Festuca ovina*, *Linnaea borealis*, *Luzula pilosa*, *Oxalis Acetosella*, *Vaccinium Myrtillus*, *Hylocomium splendens*, *Pleurozium Schreberi* och *Cetraria islandica*. I när-

Fig. 1. *Phyllodoce coerulea* (L.) Bab. Jämtlands urbergsområde. Revsunds socken: Stavre, 1950. Foto: Sölve Thulin.

heten tillkom *Empetrum hermaphroditum*. På det andra, närbelägna området växer *Phyllodoce* i ett 10-tal exemplar på en m² yta, varjämte några exemplar tillkomma ett par meter därifrån. De stå på småtuvig mark med liknande vegetation som på det förstnämnda området under en stor gran och 5—6 m från ett stort flyttblock. *Phyllodoce coerulea* har av C. A. Carlsson varit känd från Stavre från omkring år 1923. Lappljung-lokalen i Stavre ligger omkr. 300 m ö. h. inom det jämtländska urbergsområdet ej fullt tre mil från medelpadsgränsen. Jag har att tacka fil. dr Herman Persson, Stockholm, för kontrollering av mossbestämningar, jägmästare Sölve Thulin, Sundsvallsbolagen, för att han fotograferat lappljungen i Stavreskogen, då den senare kom i blomning (fig. 1), samt skogvaktare C. A. Carlsson, som för min räkning pressat *Phyllodoce* från ovannämnda lokal i Revsunds socken. Materialet har överlämnats till Riksmuseum och Uppsala Bot. Museum.

Av uppgifter om *Phyllodoce coerulea* från Jämtland må följande anföras:

Olsson (1884, s. 110): Fjällhedar, t. a., äfven på Bilsåsberget i Oviken, Bodsjöedet i Åre.

Olsson (1890, s. 39): Fjällhedar t. a., t. ex. — — —. I barrskogsregionen r. och nästan endast nära fjällen, t. ex. Huså och Fäviken vid Kallsjön, Bodsjöedet i Åre, Bilsåsberget i Oviken, norra delen af Östberget på Frösön (der en gång funnen vid klippor).

Olsson (1896, s. 135): Allmän på fjällhedar. — — — I barrskogsveg. r.: Håkafot, Huså och Fäviken vid Kallsjön, Bodsjöedet, Byhögåsen i Hallen (ett par stånd), Bilsåsberget i Oviken, Östberget norra delen på Frösön 1887 (enstaka exemplar på klippor).

Lange (1935, s. 238, 240 i fråga om Jämtlands fjällarter): »Urbergsområdet är ensamt om *Phyllodoce coerulea*, som anträffats å ett berg i Klövsjö. De övriga ha mer eller mindre talrika lokaler i både silur- och urbergsområdet.»

Lange (1938, s. 127): Berg, hedar. — Samtl. reg. — F. Allm. i de flesta specialomr. Ej antecknad från Mattmar, Myssjö, Berg. — U. Klövsjö: Staberget! (U).

Lokalerna hos Olsson och Lange hänföra sig till lappljungens förekomst i västra Jämtland, i fjällen eller deras relativa närhet. Olssons lokal från Frösön har ej upptagits av Lange, som haft tillgång till hans egenhändiga anteckningar. Olssons arbeten 1890 och 1896 grunda sig som bekant dels på hans egna undersökningar, dels på lärjungeuppgifter.

Karvik (1949, s. 159—161) lämnar några meddelanden om det anmärkningsvärda fyndet av *Phyllodoce coerulea* i Ärtemarks socken, Dalsland. Tidigare var lappljungen i vårt land ej funnen söder om Dalarnas fjälltrakter. Förklaringen till den begränsade förekomsten av *Phyllodoce* i Dalsland — ett bestånd på 3,5 m² yta — torde enligt Karvik närmast vara fröspridning genom fåglar, kanske från de relativt närbelägna sydöstnorska fjällen. Måhända kan en liknande förklaring — fröspridning genom fåglar från det jämtländska fjällområdet — tillgripas ifråga om *Phyllodoce* i sydöstra Jämtland.

Kilander (1947, s. 173—175), som funnit *Arctostaphylos alpina* i Räcksjöns kalkmyr i Sunne socken inom Jämtlands silurområde, tolkar ripbäret som relikt där. Karvik (1949, s. 161) pekar på spridning med fåglar såsom orsaken till *Arctostaphylos alpina*s uppdykande nära Ringköbing på Jylland (Romell 1938, s. 430, karta 1375 i Hultén 1950).

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Helge Stenar.

Lysimachia nemorum L. återfunnen i Tjust.

Karta 1399 i Hultén (1950) visar oss *Lysimachia nemorums* utbredning i Norden. För västerviksområdet framträder en ring, markerande att växten är utgången. Glädjande nog finns dock gularv där ännu, alltså ganska långt avlägset från växtens egentliga utbredningsområde i Norden. Följande är mig bekant om *Lysimachia nemorum* i Tjust.

I äldre floror, t. ex. Hartman (10:e uppl. 1870, s. 70, 71), anges för *Lysimachia nemorum*: Vestervik vid Marnäs, enl. Ekstr. Exemplar härifrån ligga i åtskilliga herbarier, t. ex. 1863 C. F. Willd (R); 8.8. 1863 C. E. Liljenstolpe (i Liljenstolpes herbarium på Ogestad i Odensvi sn, Tjust); Juli 1864 Eric Wahlén (R); 1865 Willd (R, U); 1865 Herb. C. M. Nyman (R); 6.9. 1868 A. P. (F.?) Gustafsson (R). Den med västervikstraktens kärlväxter väl förtrogne fil. dr A. A. W. Lund har insamlat gularv i en skog vid Marsbäcken nära Västervik: 10.8. 1878 (anteckning i Neumans flora av min broder lektor Harry Svensson), 16.7. 1900 (R), 9.7. 1903 (R, U). Vid Marsbäcken har gularv också insamlats 17 juli 1904 av Johan Berggren (R). I sitt exemplar av Pointsförteckning över Skandinaviens växter I. Fanerogamer och Kärlkryptogamer, Lund 1891, har dr Lund antecknat »skog vid Marsbäcken» för *Lysimachia nemorum*. Telegrafkommissarie C. E. Gustafssons manuskript uppger om växten: »af doktor Axel W. Lund tagen vid ett stenbrott nära Källsåker i Törnsfalla socken. Ehuru jag fått ungefärliga växtplatsen mig meddelad, har jag på grund af stenbrottens nuvarande stora antal icke kunnat återfinna densamma. Något tvifvel om uppgiftens korrekthet föreligger dock icke.» Lundin (1933, s. 16, 1936, s. 21) skriver: »Uppgiven för Marnäs men ej av mig återfunnen.»

Då jag i somras botaniserade i Tjust, hade jag uppmärksamheten riktad på eventuell förekomst av gularv i trakten av Marsbäcken. På en exkursion den 12 augusti hade jag turen att finna växten på, som jag tror, dr Lunds lokal. Jag cyklade från Gäddeglo i Törnsfalls socken på den väg, som leder till Marsbäcken. Sedan man kommit förbi den lilla gården Sandalia vid nämnda väg, är man inne i västerviksområdet. Omkring 50 m nedanför en svagt sluttande backe passerar man då en sumpig svacka i gammal vacker barrskog, mest med gran. Till höger om vägen stå vid vägkanten yppiga exemplar av *Equisetum pratense* och ett litet bestånd av *Milium effusum*. I ett småtuvigt stråk härintill växer gularv på de fuktiga områdena mellan tuvor och trädrötter i stor myckenhet mellan vägen och upp

till en omkring 20 m från denna belägen liten sumpmark. Denna hyser *Sphagnum* sp., *Thelypteris Phegopteris*, *Glyceria fluitans*, *Carex fusca*, *Alnus glutinosa*, *Ranunculus Flammula* ssp. *eu-Flammula*, *Potentilla palustris*, *P. erecta*, *Viola palustris*, *Lysimachia vulgaris* och *Cirsium palustre*. I sänkorna, ett dussintal små oregelbundna fält av någon m² yta vartdera, mellan tuvor och trädrötter utbreda sig de rika gularvmattorna, som oftast äro nästan allenarådande där — sparsam *Mnium hornum* (det. dr Herman Persson, Stockholm) är den enda mossa, jag antecknat härifrån. Granskogen innehåller små inslag av enbuske, lågvuxen tall, asp, sälg, björk, ek och rönn. Mäktiga ruggar av *Athyrium Filix-femina* äro de mest framträdande elementen mellan sänkorna, men även *Pteridium aquilinum*, *Dryopteris austriaca* ssp. *eu-spinulosa*, *Thelypteris Phegopteris*, *Th. Dryopteris*, *Oxalis Acetosella*, *Vaccinium Vitis-idaea*, *V. Myrtillus* och *Trientalis europaea* finnas. Till det nämnda huvudområdet för *Lysimachia nemorum* anknyter sig ca 10 m därifrån åt Marsbäckhållet inom omkr. 25 m² yta ett par liknande gularvfält i skogen med dess starkt framträdande *Melampyrum pratense*. De sträcka sig alldeles intill vägen. Från sistnämnda *Lysimachia nemorum*-område antecknades: *Sphagnum* sp. spars., *Equisetum pratense*, *Pteridium aquilinum*, *Athyrium Filix-femina*, *Deschampsia caespitosa*, *Anemone nemorosa*, *Rubus idaeus*, *Viola Riviniana*, *Chamaenerion angustifolium*, *Vaccinium Vitis-idaea*, *V. Myrtillus*, *Ajuga pyramidalis* och *Lactuca muralis*.

Till vänster går, strax innan man kommer till gularvområdet, en avtagsväg ner till Gamlebyviken. Några *Rubus*-buskar med vackra skära blommor stå vid vägavtaget, och ett stycke längre ned finns ett stort bestånd av *Milium effusum*. Till höger om denna avtagsväg fortsätter ner mot ett litet »svart granitbrott» svackan med, som man tycker, goda växtbetingelser i de sumpiga små stråken för gularv, i vilka den dock förgäves eftersöktes. Avtagsvägen leder ner till en utskeppningsplats för dioritblock för de Flinkska stenhuggerierna i Västervik. I den torra skogskanten nära Gamlebyviken blommade ett ansenligt bestånd av *Chimaphila umbellata*.

Avståndet mellan *Lysimachia nemorum*-lokalen och Marsbäckens gård är omkring 700 m.

Marnäs-markerna, ej så långt avlägsna från Marsbäcken och för vilka gularv — ävensom penningarv (Dahlgren 1922, s. 139) — uppgivits, hann jag ej med att genomleta den gångna sommaren. Till en del falla de inom S:ta Gertruds sjukhusområde och äro nu till stor del kulturpåverkade. Områden, där västerviksskolpojkar för ett fyrtiotal år sedan samlade *Polygonum viviparum*, *Cardamine amara*, *Chrysosplenium alternifolium*, *Crepis praemorsa* m. m. intas nu av trädgårdsanläggningar. Det återstår att se, om gularv även kan anträffas inom Marnäsområdet eller annorstädes i trakten.

Den av mig besökta lokalen för *Lysimachia nemorum* måste betraktas som rik, och någon fridlysning av växten i Tjust synes ej behöva ifrågakomma. En vettig botanist skattar ju sällsyntheter varsamt. Men även om en rovsamlare skulle komma på den befängda idén att pressa ett femtiotal ark av gularv från den skildrade lokalen, skulle väl knappast mer än ett av de tolv till fjorton »fälten» behöva spolieras.

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Helge Stenar.

Juncus beringensis Buch. och J. arcticus Willd., två nya värdväxter för Coleophora caespititiella Zeller.

Knapptågssäckmalens, *Coleophora caespititiella* ZELLER, kokongliknande larvsäckar påträffas ofta och vanligen i stort antal under höstmånaderna på *Juncus conglomeratus* L. och *J. effusus* L. Lektor F. HÅRD AV SEGERSTAD har i samarbete med den kände coleophoridspecialisten fil. dr P. BENANDER, Höör, i »Zur Systematik und Biologie von *Juncus effusus* L. und *J. conglomeratus* L.» (Acta Horti Gothoburgensis, XIV, 1940) lämnat viktiga bidrag till dessa tågarters och knapptågssäckmalens biologi. HÅRD konstaterade under flera år att praktiskt taget alla bestånd av *J. conglomeratus* hyste ett mycket stort antal larvsäckar, under det att fjärilslarverna voro färre till antalet på *J. effusus* eller i vissa trakter helt saknades på denna art. Larvernas antal ökades längre fram på hösten hos *J. effusus*, och BENANDER och HÅRD tolka detta så att larvernas utveckling sker långsammare på denna art. Enligt HÅRD föreligger ingen större anatomisk olikhet i fruktväggarna hos knapptågen och veketågen, varför inget iakttagbart hinder finnes för larvernas inträngande i den senare artens frukter. Då fjärilarna även svärmade rikligt under veketågens blomningstid, som inträffar något senare än blomningstiden för *J. conglomeratus*, kan tydligen disproportionen i larvsäckarnas antal ej tillskrivas de olika blomningstiderna. Kemisk olikhet i konstitutionen hos de båda arterna diskuteras även av HÅRD, som skriver:

»2) Chemische Verschiedenheiten.

a) Diese können entweder als positiv wirksam vorgestellt werden, dergestalt etwa dass irgendein für uns nicht wahrnehmbarer Duft bei *J. conglomeratus* das Schmetterlingsweibchen dorthin zieht.

b) Anderseits könnte man sich auch eine negative Einwirkung gewisser schädlicher Stoffe in der Fruchtknotenwand bei *J. effusus* denken, die die Raupen am Eindringen hindern würde, falls Eier dort abgelegt wurden; auch die Samen könnten schädlich sein.»

Att någon olikhet i blomdoften hos dessa *Juncus*-arter skulle spela någon roll tror ej HÅRD på, då larverna även leva på systematiskt så vitt skilda arter som *J. compressus*, *J. lampocarpus*, *J. alpinus* ssp. *nodulosus* och *J. squarrosus*.

Till ovan uppräknade värdväxter för *Coleophora caespititiella* ZELLER kan jag tillfoga *Juncus beringensis* BUCH. och *J. arcticus* WILLD., på vilka jag under flera höstar i Bergianska trädgården iakttagit de blekgula larvsäckarna. Dr BENANDER har varit nog vänlig att hösten 1951 kontrollbestämma de till honom översända larvsäckarna. Mina båda *Juncus*-arters utbredningsområden ligga visserligen helt utanför fjärilens kända utbredningsområde, men jag har ändå ansett det vara värdefullt med ett meddelande om dessa nya värdväxter för ifrågavarande *Coleophora*-art, främst med tanke på HÅRDS diskussion om *Juncus*-arternas kemiska konstitution. Det i Bergianska trädgården angripna beståndet av *J. arcticus* härstammar från Abisko, varest fil. dr ERIK ASPLUND insamlade det år 1946. Materialet av *J. beringensis* har dragits upp ur frön, som år 1941 erhöllos från botaniska trädgården i Sapporo, Japan. Denna arts utbredningsområde sträcker sig från norra Kamtschatka och Ochotsk till Jeso och Honshu.

Juncus-släktet omfattar enligt F. VIERHAPPER (*Juncaceae* i ENGLER, A. und PRANTL, K., Nat. Pflanzenfam., Bd 15 a, 1930) 225 arter fördelade på sex sektioner. Angrepp av *Coleophora caespititiella* ha av BENANDER, HÅRD och undertecknad konstaterats på nedan uppräknade arter ordnade sektionsvis.

Sekt. I. *Poiophylli: J. compressus* JACQ., *J. squarrosus* L.

Sekt. II. *Genuini: J. arcticus* WILLD. (cult.), *J. beringensis* BUCH. (cult.), *J. conglomeratus* L., *J. effusus* L., *J. filiformis* L.

Sekt. V. *Septati: J. alpinus* VILL. ssp. *nodulosus* (WG) LINDM., *J. lampocarpus* EHRH.

Erik Söderberg.

Crambe maritima L. funnen på två lokaler i Södermanland.

Vid en exkursion till ön Järflotta strax S. om Nynäshamn i Ösmo socken den 25.7.1946 fann jag ett exemplar av strandkål, *Crambe maritima* L., vilken växt tidigare ej är känd från Södermanland. Fyndet gjordes på den steniga stranden vid Lökvik på öns östra sida, där ett enda ungt, men ganska kraftigt exemplar påträffades. Någon blomning ägde ej rum det året. Lokalen besöktes sedan 1948 och 1949, och då hade plantan vuxit i storlek men blommade inte heller något av dessa år. Nästa besök på platsen gjordes den 7 oktober i år, och då anträffades ytterligare 2 mycket unga exemplar i omedelbar närhet av den gamla plantan, som fortfarande är kraftig och växtlig, men som inte heller detta år hade blommat.

Den 11.9.1951 företog jag tillsammans med fil. dr. ERIK ASPLUND en exkursion till Torö, och vi gjorde då ett nytt fynd av *Crambe maritima* på stenstranden Ö. om Örudden Endast ett ungt exemplar påträffades, av

vilket ett blad insamlades som beläggexemplar till Riksmuseet. Denna lokal är belägen cirka 1 mil SV om den föregående.

Enligt »Stockholmstraktens växter» 2:a uppl. är *Crambe maritima* tidigare sporadiskt funnen på sammanlagt 5 lokaler i Stockholms skärgård, samtliga belägna i Uppland. De senaste kända fynden gjordes 1929 vid Sandhamn och på Hästskär i Djurö socken. Fast förekomst har arten närmast på Åland, Gotland och Öland, men däremot är den längs kusten förutom på ovannämnda lokaler ej känd norr om Kristianopel i Blekinge (Holmgren 1942). På de nu upptäckta lokalerna är arten säkerligen nyinvandrad, i annat fall borde den med all sannolikhet ha uppmärksammats tidigare, då båda lokalerna på grund av sin rika havsstrandflora varit flitigt besökta av botanister. Fyndet på Järflotta har tidigare meddelats till professor Eric Hultén och är medtaget i hans atlas.

Einar Pettersson

RECENSIONER.

G. Huber-Pestalozzi: Das Phytoplankton des Süsswassers. 3. Teil. Cryptophyceen, Chloromonadinen, Peridineen. (Die Binnengewässer, Band XVI, 3. Teil) E. Schweizerbart'sche Verlagsbuchhandlung. Stuttgart 1951. — Häftad DM 67: —, bunden DM 70: —.

Även om biologien och medicinen är så närbesläktade att de fordom gällde som ett enda forskningsområde, hör det numera nog inte till vanligheterna att en praktiserande läkare gör en grundläggnade insats inom en rent biologisk deldisciplin. Detta är emellertid vad den nu 74-årige schweiziske urologen Dr. phil. et med. Gottfried Huber-Pestalozzi har gjort och gör genom sitt stora arbete »Das Phytoplankton des Süsswassers», varav den fjärde volymen nyligen utkommit. På 310 sidor och 69 planscher, med 1415 figurer, behandlas här:

kryptofycéerna	med	63	arter,	5	varieteter	och	2	former,
chloromonaderna	»	9	»	—	»	»	—	» ,
peridinéerna	»	164	»	30	»	»	77	» .

Det är lätt att inse vilka svårigheter författaren har haft att övervinna innan hans manuskript blev tryckfärdigt. Den taxonomiska fytoplanktonforskningen har gjort stora framsteg sedan de senaste sammanfattande bearbetningarna, främst i Paschers »Süsswasserflora» och Rabenhorsts »Kryptogamenflora», kom ut — delvis för nära 40 år sedan. Men de nya rönen har publicerats i vitt skilda facktidskrifter och perodica, ofta mycket svåråtkomliga, och det gällde därför för författaren att under kritisk sovring sammanställa och till någotsånär enhetliga system sammansmälta de otaliga detaljuppgifterna. I många fall måste helt nya bestämningstabeller upprättas, inte bara för arter och varieteter utan ofta även för bestämningen av släktet. Egentligen kan endast den som har arbetat eller har försökt att arbeta med de subtila organismer som här beskrivas känna den riktiga tacksamheten för Huber-Pestalozzis monografi. Dess betydelse för allt framtida studium av sötvattnens planktonalger kan knappast överskattas.

Visserligen är det föreliggande arbetet främst avsett som hjälpmedel vid algernas bestämning men förf. förklarar själv (s. 112) att han anser det vara »ein Erfordernis der Zeit, dass wir nicht nur neue Formen beschreiben, sondern ihre Kenntnis auch ökologisch untermauern». I enlighet härmed finner läsaren efter nästan varje artbeskrivning en kort sammanfattning av vad som är känt angående artens utbredning och ekologi m. m. Denna uppläggning ökar givetvis verkets värde men man får samtidigt ett starkt

intryck av hur litet vi egentligen ännu faktiskt vet på detta område. Men man har kanske rätt att hoppas på en snabbt stigande kurva för kännedomen om de enskilda fytoplankternas ekologi, sedan deras ofta så besvärliga bestämning nu blivit avsevärt underlättad tack vare Dr. med. Huber-Pestalozzis allt annat än amatörmässiga insats på botanikens område.

Wilhelm Rodhe.

Täckholm, Vivi, Täckholm, Gunnar, and Drar, Mohammed, Flora of Egypt. — Vol. I. Pteridophyta, Gymnospermae and Angiospermae, part Monocotyledones: Typhaceae — Graminae. By Vivi and Gunnar Täckholm in collaboration with Mohammed Drar. Bull. Fac. Sci. Fouad I Univ., 17. Cairo 1941. 574 pp. — Vol. II. Angiospermae, part Monocotyledones: Cyperaceae — Juncaceae. By Vivi Täckholm and Mohammed Drar. Ibid., 28. Cairo 1950. 537 pp.

Egypten är ju ett av de äldsta kulturländer man känner. Den ursprungliga växtvärlden här, en nordafrikansk stäpp-, öken- och alluvialflora, har under mer än sex årtusenden utarmats, omformats, berikats av mänsklig odling och samfärdsel. Detta gäller givetvis i stor utsträckning även andra delar av Medelhavsbäckenet, men kanske dock ingenstädes så utpräglat som här, bl. a. beroende på en hög befolkningstäthet och långvarig intensiv uppodling inom ett geografiskt mycket begränsat område. Naturlig vegetation finns endast i ringa utsträckning bevarad inom landets gränser. Jämförelsevis orörda är ännu de östliga torrområdena med sin typiskt nordafrikanska ökenflora, till stor del bestående av vinterannueller. Sin ursprungliga prägel bär också Sinaibergens märkliga Irano-Turaniska flora längst i nordost. Acacia-skogarna på Elba Mts längst i söder är vidare tämligen orörda; på denna enda punkt överskrider den nubiska floran landets gränser. Men överallt annars, t. o. m. i kanalernas rika högre vattenvegetation gör sig mänskligt inflytande starkt märkbart.

Detta inflytande speglar sig i det här anmälda arbetet framför allt på trenne sätt. De odlade växterna har behandlats synnerligen utförligt, i mångas ögon har de säkerligen fått sig ett oproportionerligt stort utrymme tillmätt. Ett stort antal arter har vidare påträffats i den s. k. gravfloran, en arkeologisk-botanisk källa om vilken Egypten är ensamt. Fynd av dylik art relateras och diskuteras med stor utförlighet. Slutligen omnämnes artens eventuella användning inom den egyptiska farmakopén, ett ämne med en omfångsrik, till övervägande delar på arabiska avfattad litteratur. Skillnaden mot en mer konventionellt avfattad flora blir sålunda betydande. Så behandlas palmerna, varav endast en art (*Hyphaene thebaica* (L.) Mart.) förekommer som spontan, på ca 170 sidor. Dadelpalmen ensam upptar 110 sidor. Avsnittet om *Phoenix dactylifera* — till stora delar författat av Drar — kan f. ö. tjäna som ett typiskt exempel på den ovanligt detaljerade framställningen av kulturväxterna. Efter en kort redogörelse för synonymer och morfologi följer först ett huvudavsnitt om dadelpalmen i det moderna Egypten. Det är disponerat under femton delrubriker och behandlar utbredningen i landet, totalproduktion, export och

taxering, könlig och vegetativ förökning, bevattning, tillväxt, beskärning, föryngring, olika pollineringsmetoder, mognad, skörd och konservering, användning i industri och hushåll, varieteter under odling, sjukdomar samt en samtida arabisk dadelpalmsterminologi (91 termer). Dadelpalmen i det forntida Egypten behandlas i ett annat huvudkapitel på samma utförliga sätt. Denna monografi över dadelpalmen i Egypten avslutas med en överväldigande litteraturlista med omkring 360 titlar (därav ca 60 på arabiska avfattade arbeten) från Herodotos och Theophrastos till de senaste årens auktoriteter.

I viss motsats till all denna utförlighet står de kortfattade diagnoserna och de synnerligen lapidariska bestämningstabellerna. Författarna har nämligen i sin allmänna uppställning följt Boissiers bekanta »Flora Orientalis», och har följaktligen hänvisat till de utförligare diagnoserna där. Under varje familj har sammanförts en förteckning över den viktigaste litteraturen (taxonomi, fylogeni, morfologi och i vissa fall fysiologi, samt farmaceutisk och lingvistisk litteratur). Denna del av arbetet har helt ålegat Vivi Täckholm.

Utbredningsuppgifterna är värda en särskild honnör. Redan under den första vistelsen i Egypten (1925—29) gjorde Vivi och Gunnar Täckholm omfattande insamlingar. De bestämdes senare av Vivi Täckholm, som under 1930-talet granskade och reexaminerade det jättelika material från Egypten, som ackumulerats i olika europeiska museer, främst de i Berlin, Genève, botaniska trädgården i Kew, och British Museum. Allt detta har inarbetats i den redogörelse, som ges för utbredningen av varje art. Lokaluppgifterna är i flertalet fall detaljerade och ordnade efter växtgeografiska provinser. Under den inomegyptiska utbredningen redovisas också de förnämliga resultaten av det fältarbete som under senare år bedrivits av Mohammed Drar under exkursioner till landets olika delar. Presentationen av varje art avslutas med en fyllig redogörelse för dess utbredning utanför Egypten. Var och en som sysslat med tropiska växters geografi, vet hur svårt det är att ur den existerande litteraturen få en adekvat bild av en viss arts utbredning. Att kritiskt sålla och väga det existerande litteraturmaterialet är ett mödosamt, tidskrävande och otacksamt arbete. De noggranna totalutbredningsuppgifterna är en av detta floraverks allra väsentligaste förtjänster.

Flora of Egypt är ett rätt egenartat konglomerat av upplysningar. Dess största svaghet torde ligga i det något oförmedlade och för den oinvigde överraskande sätt varpå floristik, arabisk språklära, agrikultur, släktdiagnoser, egyptologi, hushållslära, etc. blandas med varandra i texten. Man konsulterar ju vanligen en flora för att skaffa sig information angående en viss spontan art från området, hur den ser ut, hur den går att skilja från andra arter, och var den finns inom och utom området. Dessa upplysningar kan man också förskaffa sig här, men man får ofta leta efter dem; de har nämligen en viss tendens att drunkna i det överväldigande materialet av fakta från andra områden. Å andra sidan kan man förstå att den egyptiska växtvärlden har inbjudit till en framställning av detta slag: här har skillnaden mellan spontant och icke spontant i viss mån utplånats genom årtusendenas nötning. Sannolikt har författarna också varit

tvungna att i viss mån taga hänsyn till den orientaliska inställningen till botaniken som en nyttovetenskap.

De hittills utkomna volymerna har tillkommit som resultatet av ett team-work mellan Vivi och Gunnar Täckholm samt Mohammed Drar. Många eminenta forskare — uppräknade i inledningen till den första delen — har bidragit med hjälp och upplysningar. Bland botanister nämns särskilt Alex Aaronsohn, Robert Chodat, J. F. Lewis och Gunnar Samuelsson. Under senare år har väl Erik Asplund varit den främste rådgivaren. Men trots allt samarbete mellan tre författare, vetenskapliga institutioner och talrika enskilda forskare, är detta monumentala verk dock präglat av en persons entusiasm inför uppgiften. I väsentlig grad har Vivi Täckholm här själv byggt sig ett monument — *aere perennius*.

Henning Horn af Rantzien.

Vavilov, N. I., The Origin, Variation, Immunity and Breeding of Cultivated Plants. Transl. from Russian by K. Starr Chester. — Waltham, Mass. (: The Chronica Botanica Co.; Uppsala: A. B. Lundequistska Bokhandeln) 1951. 364 pp., ill. Pris $ 7.50.

Vavilovs studier över kulturväxterna utgör ett av de mest bekanta bidragen till den tillämpade botaniken under detta sekel. Det viktigaste av Vavilovs forskningar på detta område finns medtaget i handböckerna för universitetsbruk; hans arbeten är kända över hela jorden och behöver sålunda ingen närmare presentation.

Grundvalen för den framställning som nu utgivits på engelska är ett symposium på över 2500 sidor, The Scientific Bases of Plant Breeding, som utkom 1935 med Vavilov som utgivare och som författare av den övervägande delen av texten. I detta verk framlades i sin mest fullständiga form författarens studier över kulturväxternas ursprung, lagen om de homologa variationsserierna, kulturväxternas immunitet mot sjukdomar och grundvalarna för förädlingen av odlade växter, främst vete. De väsentliga delarna av detta symposium har nu överförts till engelska och försetts med illustrationer ur Vavilovs egna arbeten.

Den anmälda sammanfattningen är indelad i fyra huvudavsnitt, vart och ett med en utförlig litteraturförteckning, vartill kommer en jättelik bibliografi över vete och dess förädling allena i slutet av boken, omfattande 19 sidor fin stil.

Det första huvudavsnittet behandlar de växtgeografiska grundvalarna för växtförädling. Här diskuteras främst kulturväxternas olika uppkomstcentra. Förf. forskningar inom detta område torde vara välkända. Vavilov urskiljer 11 olika huvudcentra, nämligen China, Indien, Indo-Malaya, Centralasien, Främre Orienten, Medelhavsområdet och Abessinien, samt inom Nya Världen, Sydmexiko-Centralamerika, Ecuador-Bolivia-Peru, ön Chiloe samt Sydbrasilien-Paraguay. De väsentliga delarna av den Vavilovska läran om kulturväxternas ursprung publicerades i en för oss tillgänglig språkdräkt redan 1928 (Die geographischen Genzentren der Kulturpflanzen, Verh. V. Int. Congr. Vererbungwiss.); denna tidigare

framställning har här kompletterats på ett antal punkter. I denna första del av boken diskuteras också en del viktiga förutsättningar för införsel av främmande kulturväxtmaterial till nya geografiska områden; vidare ges en koncentrerad framställning av vernalisationen och dess betydelse.

I de två följande huvudavsnitten behandlas den homologa variationen — också den ett vidareutvecklande av ett tidigare tema, det nu klassiska arbetet The Law of Homologous Series in Variation (Jour. Gen. 12, 1922) — och kulturväxternas immunitet. Det senare problemet har fått en mycket utförlig behandling och diskuteras både ur teoretisk och praktisk synvinkel. Kapitlen om immunitetens natur, om förvärvad immunitet och om dess förhållande till yttre faktorer är utomordentligt intressanta även ur en vidare aspekt; samma omdöme gäller avsnitten om de patogena parasiternas art- och rasbildning.

Den sista delen av boken behandlar enbart förädlingen av vete och omfattar ungefär hälften av antalet sidor. I de första kapitlen skildras de olika arterna och raserna taxonomiskt, växtgeografiskt och variationsanalytiskt. Så följer en inträngande analys av vetets ekologi under naturliga och artificiella förhållanden med särskild tonvikt på dess ekologiska plasticitet. Ett särskilt kapitel är ägnat *Triticum*-arternas blombiologi. De genetiska förhållandena är vidare mycket utförligt behandlade. Ur skildringen av vete från dessa tre synpunkter, den taxonomisk-växtgeografisk-variationsanalytiska, den ståndortsekologisk-klimatologiska och den cytologisk-genetiska, växer så behandlingen av den planmässiga förädlingen fram: vad som redan uppnåtts och riktlinjerna för fortsatta arbeten. Hela avsnittet avslutas med en framställning av odling och förädling av detta sädesslag i de veteproducerande länderna.

Den ryska upplagan av Vavilovs arbete trycktes för 16 år sedan och inga försök har gjorts från översättarens eller förlagets sida att bringa framställningen up to date. Detta torde vara särskilt märkbart evad gäller de rent genetiska kapitlen och skildringen av vetets odling och förädling i olika länder. Sedan 1935 har ju en ny insyn vunnits i många ärftlighetsprocesser och vissa tidigare uppfattningar har måst revideras. Därigenom har naturligtvis Vavilovs framställning av växtförädlingen kommit att sakna ett antal viktiga metoder, som idag står genetikerna till buds (t. ex. påverkan av mutationsfrekvensen genom en rad olika agens).

Henning Horn af Rantzien.

Lawrence, George H. M., Taxonomy of Vascular Plants. — New York (The Macmillan Co.) 1951. 823 pp. 322 fig. Pris $ 7.95.

I närmast föregående häfte av denna tidskrift (sid. 541) anmälde dess redaktör en förra året utkommen handbok över dikotyledonernas klassificering, utgiven av den under lång tid vid Brooklyn Botanic Garden verksamme systematikern Alfred Gundersen. Redan har ett nytt amerikanskt arbete rörande de högre växternas systematik sett dagen, denna gång med professorn i botanik vid The Bailey Hortorium, Cornell Univer-

sity, GEORGE LAWRENCE som författare. Då dennes bok till sin uppläggning avviker både från GUNDERSENS och andra existerande handböcker och läroböcker i ämnet, förtjänar den här ett omnämnande.

Boken är uppdelad på två huvuddelar. Den första (331 sid.) behandlar växtsystematikens teori och praktik och sönderfaller i 13 kapitel. I inledningen lämnas en kort redogörelse för systematikens (taxonomiens) innehåll och för innebörden av växtbestämning, nomenklatur, klassificering och fylogeni, varefter systematikens betydelse i olika sammanhang påvisas och en historik lämnas över de intill senaste tid gjorda försöken till en klassificering av kärlväxterna. I ett därpå följande kapitel »Principles of Taxonomy» behandlar förf. de taxonomiska enheterna, förklarar dessas innebörd (jämte den av VII. Internationella botaniska kongressen antagna termen »taxon») och diskuterar olika slag av morfologiska egenskaper med avseende på deras evolution och värde för växternas klassificering. Utrymme har också beretts åt fylogenien, med angivande av dess förhållande till taxonomien, skilda botaniska vetenskapsgrenars bidrag i detta sammanhang samt viktigare teorier rörande pteridofyternas, gymnospermernas och angiospermernas evolutionshistoria. I anslutning till den nyss nämnda historiken jämför LAWRENCE mera ingående senare tiders klassificeringssystem med varandra (BENTHAM & HOOKER, HALLIER, ENGLER, BESSEY, HUTCHINSON och TIPPO) och tager därvid även hänsyn till viktigare modifikationer av dessa, utarbetade av WETTSTEIN, RENDLE, PULLE och SKOTTSBERG. Han vill där förklara de principer, som ligga till grund för dessa system, påvisa olikhe' rna i anordningen av de högre taxonomiska enheterna, ange systemens starka och svaga sidor och ge en uppfattning om, i vilka riktningar det fylogenetiska tänkandet rört och rör sig. LAWRENCE antyder sannolikheten av att ett nytt system snart kan komma att framläggas, som bättre än något tidigare harmonierar med resultaten av de senare årens omfattande forskningar på skilda områden. I närmast följande kapitel behandlas växtgeografiens betydelse för systematiken, med korta hänvisningar till teorier rörande jordskorpans byggnad och förändringarna i jordytans konfiguration, vidare till växtvärldens utvecklingshistoria, till den fysiska geografiens betydelse för växternas utbredning och till den dynamiska växtgeografiens teoretiska grundvalar. Efter ytterligare ett kapitel om biosystematik och cytogenetik övergår förf. till att behandla växtnomenklaturen, dess historia och senaste utformning, metoderna för växtbestämning, insamling och uppbevaring av växtmaterial ävensom för utarbetandet av systematiska monografier och revisioner samt floror. Denna första huvuddel av boken avslutas med ett kapitel om den växtsystematiska litteraturen, med angivande av viktigare indices, världsfloror, regionala floror, bibliografier, refererande tidskrifter, tidskrifter med originalarbeten av systematisk karaktär, handböcker över odlade växter o. s. v. Dessutom har vart och ett av ovannämnda kapitel försetts med en kort litteraturförteckning, som anvisar vägen till en grundligare orientering på respektive områden.

Den andra huvuddelen (400 sid.) av LAWRENCES arbete innehåller en systematisk förteckning över de 264 kärlväxtfamiljer, som genom nu levande inhemska eller införda arter äro representerade i Nordamerika norr om Mexiko. Förf. har därvid följt ENGLER & DIELS, »Syllabus der Pflanzen-

familien» (1936) beträffande ordningen mellan familjerna och endast infört den ändringen, att växtgrupper, som på senare tid upphöjts till rang av familjer ha accepterats som sådana. Han betonar att valet av system uteslutande skett av vissa praktiska hänsyn, som närmare angivas i inledningen. För varje familj lämnas icke blott en karakteristik jämte summariska uppgifter om sammansättning, geografisk utbredning och ekonomisk betydelse utan dessutom en sammanfattning av nyare åsikter om familjens systematiska ställning och fylogeni samt en hänvisning till viktigare litteratur. Härigenom avviker Lawrences arbete mycket fördelaktigt från andra systematiska handböcker, där familjerna ofta nog behandlats utan närmare motivering för den valda ordningsföljden. Ehuru paleobotaniken och dess resultat ofta åberopas i bokens allmänna huvuddel, äro de fossila växterna uteslutna ur den systematiska förteckningen, och ej heller ha där annat än i undantagsfall hänvisningar till den paleobotaniska litteraturen lämnats. Under *Ginkgoaceae* t. ex. anföres icke något av de senare arbetena om utdöda ginkgoväxter, vilket hade varit önskvärt för att ge det riktiga perspektivet på denna märkliga växtgrupp, men däremot ej mindre än fem uppsatser om släktnamnet *Ginkgo* och dess uppkomst och rätta stavning.

Både den första och, särskilt, den andra huvuddelen av boken är rikligt försedd med väl utförda och instruktiva illustrationer, av vilka många utgöra original. Korrekturläsningen av texten tycks ha skett i stor hast att döma av de tryckfel, som finnas här och var.

Förutom huvuddelarna finnas två bihang. I det ena lämnas ett förslag till en inledande universitetskurs i systematisk botanik bestående av 30 föreläsningar med tillhörande laborationer. Det andra är en illustrerad förteckning över i systematiken och speciellt i det föreliggande arbetet nyttjade termer med förklaringar.

Såsom antytts genom den lämnade översikten har detta arbete ett mycket rikt och värdefullt innehåll. Lawrence understryker att växtsystematiken inte bara består i bestämning och namngivning av växterna utan dessutom har att befatta sig med deras klassificering och att den särskilt i det avseendet är en vetenskap, som ställer stora krav på sina utövare. Ett behärskande av systematiken i vid bemärkelse och alla dess arbetsmetoder förutsätter egentligen förutbildning och erfarenhet inom en hel rad grenar av botaniken, isynnerhet morfologi, anatomi, cytologi, genetik, paleobotanik och växtgeografi. I praktiken är detta knappast möjligt att uppnå för någon. Men en lärobok i systematisk botanik bör taga åtskillig hänsyn till den kunskap om växterna, som dessa grenar förmedlat, och det är just vad som skett i Lawrences bok. På ett begränsat utrymme har det lyckats förf. att ge en förträfflig och intresseväckande framställning av växtsystematiken i modern mening. Boken kommer säkerligen att få stor användning i den akademiska undervisningen i systematisk botanik. Den kan överhuvudtaget anbefallas var och en, som vill förvärva en inblick i den systematiska botanikens problem, arbetsmetoder och hittills uppnådda resultat beträffande klassificeringen av de nu levande kärlväxterna.

Rudolf Florin.

Phytomorphology, an international journal of Plant Morphology, Vol. 1, Nos. 1—2, August 1951. Edited by P. Maheshwari, University of Delhi, Delhi 8, India. Published by the International Society of Plant Morphologists. — 152 sid. Pris 1 £ 5 s (London).

»The International Society of Plant Morphologists» grundades den 4 januari 1951 vid den »Pan-Indian Ocean-Science Congress», som vid den tiden hölls i Bangalore, Indien. Sällskapets syfte är att befrämja det internationella samarbetet inom den botaniska morfologien, anatomien och embryologien i vidaste bemärkelse. Tidskriften »Phytomorphology» är sällskapets officiella organ. Under förutsättning av tillräckligt ekonomiskt stöd, isynnerhet genom att institutioner subskribera på tidskriften [pris 2 £ 10 s (London)] och genom ökning av antalet medlemmar i sällskapet (årsavgift 2 £, ständig medlemsavgift 20 £), hoppas man bliva i stånd att utge 4 häften om året med 100 sidor i varje häfte. Anmälningar mottagas av professor P. Maheshwari, Department of Botany, University of Delhi.

Ett första dubbelhäfte av »Phytomorphology» har just utkommit. Innehållet är rikt och omväxlande. C. W. Wardlaw (Manchester) behandlar växternas morfogenes och allmänna organisation, Alma G. Stokey (South Hadley, Mass.) gamofytkaraktärernas betydelse för de homospora ormbunkarnas klassificering, E. Battaglia (Montreal) angiospermernas han- och hongamofyter och deras fylogeni, I. W. Bailey (Cambridge, Mass.) de anatomiska karaktärernas användbarhet vid studiet av högre växters fylogeni och klassificering, J. Parkin (Blaithwaite, Wigton) ståndarnas evolution hos angiospermerna samt T. M. Harris (Reading) den utdöda växtgruppen *Caytoniales* och dess släktskapsförhållanden. Förutom dessa uppsatser av mera allmänt intresse finner man i det nu utkomna dubbelhäftet även speciella arbeten av algologiskt, anatomiskt, cytologiskt och embryologiskt innehåll.

Tidskriften har fått en god allmän utstyrsel, vårdat tryck och utmärkta illustrationer. Uppsatserna äro denna gång genomgående författade på engelska, men bidrag mottagas i fortsättningen även på franska och tyska språken. Såsom växtmorfologiens speciella organ är tidskriften förtjänt av att få stor spridning.

Rudolf Florin.

SVENSKA BOTANISKA FÖRENINGEN.

Revisionssammanträde.

Föreningen sammanträdde den 18 april 1951 å Stockholms Högskola under ordförandeskap av professor E. Melin.

Ordföranden meddelade, att föreningen sedan föregående sammanträde genom döden förlorat två av sina medlemmar, nämligen lektor Johan Mauritzon, Hälsingborg, och missionslärare Josef Håkansson, Lidingö. Ordföranden erinrade om de bortgångnas botaniska gärning och lyste frid över deras minne.

De nya medlemmar, som av styrelsen invalts i föreningen, anmäldes.

Ordföranden meddelade, att till styrelsen ingått en skrivelse med förslag att till hedersledamot i Svenska Botaniska Föreningen välja professor Rob. E. Fries. Styrelsen ville för sin del livligt tillstyrka detta förslag. Föreningen beslöt i enlighet härmed att välja professor Fries till hedersledamot. Valet skedde med acklamation.

Revisionsberättelsen upplästes av revisor Wibom och på revisorernas hemställan beviljades styrelsen och skattmästaren full ansvarsfrihet.

Ordföranden meddelade, att föreningen av framlidne lektor J. A. O. Skårman erhållit en donation på 20.000 kronor. Donationen har tills vidare fonderats.

Professor Eric Hultén höll ett med talrika ljusbilder beledsagat föredrag över ämnet »Floran och vegetationen i eurasiatiska Arktis. En studie.»

Sammanträdet bevistades av 76 personer.

Nya medlemmar.

Vid styrelsesammanträdet den 22 februari 1951 invaldes såsom medlemmar av föreningen: på förslag av docent G. Degelius: fil. stud. Per-Olof Lindahl, Uppsala; på förslag av fil. dr G. Erdtman: fil. stud. Jaan Terasmäe, Uppsala; på förslag av läroverksadjunkt A. Jansson: läroverksadjunkt Karl H. Åkerberg, Södertälje; på förslag av konservator A. Zander: herr Carl-Erik Carlsson, Råstorp, arkivarie Kaj Rasmussen, Visby, Stadsbiblioteket, Mölndal, herr A. Huggert, Bromma, National Botanic Gardens, Kirstenbosch, Kapstaden, Kaiser Wilhelm Institut für Biologie, Biblioteket, Tübingen, skogsmästare Wilhelm Wrigstedt, Gullberna; på förslag av styrelsen: fil. lic. Carl Erman, Bromma. — Vid styrelsesammanträdet den 18 april 1951 invaldes följande medlemmar: på förslag av

fil. mag. I. Fröman: fil. lic. Arvid Hedelius, Stockholm; på förslag av fil. lic. G. Harling: trädgårdsmästare Ivar Eklundh, Stockholm; på förslag av konservator A. Zander: Västgöta Nations bibliotek, Uppsala, Kalmar Stadsbibliotek, Kalmar, fil. dr John Lagerkranz, Mälarhöjden, professorskan Elsa Kylin, Lund, Bundesanstalt für Vegetationskartierung, Stolzenau, Tyskland. — Vid styrelsesammanträdet den 26 september 1951 invaldes följande medlemmar: på förslag av professor K. V. O. Dahlgren: fil. stud. Jessie Thorburn, Västerås; på förslag av apotekare B. Danielsson: apotekare Carl Börje Darpö, Föllinge, apotekare Jan G. J. Gustafsson, Gävle; på förslag av lektor A. Frisendahl: apotekare Anders Nordesjö, Skog; på förslag av docent G. Harling: fröken Birgitta Julinder, Stockholm; på förslag av fil. lic. O. Mårtensson: civilingenjör Herman Belin, Uppsala, ingenjör Sten Sjögren, Uppsala, civilingenjör Bertil Sundbeck, Uppsala, tekn. lic. Adolf Berggren, Uppsala; på förslag av överste C.-A. Torén: fröken Elisabeth von Döbeln, Stockholm; på förslag av fru A. Wallerius: fru Brita Ehrenborg, Lidingö; på förslag av konservator A. Zander: Istituto ed Orto Botanico della Università, Pavia, Italien, laboratoriebiträde Rein Wellner, Älvsjö, Freshwater Biological Association Library, Ambleside, England.

Föreningens höstexkursion till Muskö den 30 september 1951.

Föreningen anordnade även i år en svampexkursion i Stockholmstrakten tillsamman med Botaniska Sällskapet i Stockholm, nämligen till Muskö. Detta mål hade valts bl. a. med hänsyn till att Muskö ur mykologisk synpunkt utgjorde ett nästan okänt område. En första inventering där hade sålunda sitt särskilda intresse icke minst för kännedomen om Stockholmstrakten.

Exkursionen företogs i tvenne förhyrda bussar, som från Kungstensgatan (Borgarskolan) förde de nära 60 deltagarna till Söderby brygga, varifrån överfärden skedde med båt till Gullboda på öns sydvästra del. Här gjordes nu ett kort uppehåll för medhavd lunch. Sällskapet vandrade därefter den c. 4,5 km långa sträckan till Ludvigsbergs pensionat, där en välarrangerad och animerad middag intogs under allmän tillslutning. Flertalet deltagare tog sig sedan till fots i kvällsmörkret den 1,5 km långa sträckan till Mickrums brygga, varifrån hemfärden skedde med båt till Söderby och med bussar åter till Stockholm.

Den rekordartade torkan, som under den milda, utdragna hösten gjort sig betydligt kännbar i Stockholmstrakten, hade förorsakat, att svampfloran på det hela taget var förhållandevis klent utvecklad. Under sådana omständigheter var det nödvändigt att för en ev. svampexkursion orientera sig för att finna ett gebit, som trots rådande årstid och väderleksförhållanden kunde visa sig lönande. Så hade också skett genom en förexkursion, varvid just sydvästra delen av Muskö, trakten mellan Gullboda och Mälby, hade befunnits erbjuda en möjlig utgångspunkt. Och det var i denna del av ön, som exkursionen uppehöll sig större delen av dagen. Området utgöres av tät, mossig barrskogsmark med i NNO-SSV orienterade bergsåsar och mellanliggande fuktiga dalstråk. Svampfloran var här också efter

förhållandena ovanligt rik, betydligt bättre än man haft anledning förvänta. Sålunda demonstrerades svampar av skilda grupper med bistånd av professorerna Rob. E. Fries, T. Lagerberg, E. Melin, assistent E. Ingelström, lektor H. Kökeritz och undertecknad, de båda sistnämnda i egenskap av exkursionsledare. Sammanlagt annoterades ett 100-tal arter eller något mera och tillvaratogs beläggmaterial för fynd av intresse. Det rörde sig dock med få undantag om mera allmänt utbredda arter eller sådana som förut voro kända från likartade områden i Stockholmstrakten. Ur anteckningslistan må här nämnas följande: *Lentinus omphalodes* (på gammal ved), *Cortinarius* (*Phlegmacium*) *cumatilis*, *C.* (*Ph.*) *percomis*, *C.* (*Inoloma pholideus*, *C.* (*Telamonia*) *laniger* (alla i mossig barrblandskog), *Clitopilus hirneola* (flerstädes på sandiga skogsstigar), *Lactarius spinosulus* (under björk), *Polyporus nidulans* (på björk) o. s. v. Invid Ludvigsberg anträffades *Psilocybe semilanceata* i en betesmark, i sydliga Sverige flerstädes ganska vanlig men sällsynt i Stockholmstrakten. Den har likväl i år anträffats på flera lokaler härstädes. Ett på grund av samma orsak anmärkningsvärt fynd var *Lactarius hysginus*, som förekom ganska rikligt på en sandig skogsstig S om Malmen.

Gustaf E. Haglund.